

Cours d'Été O.T.A.N.

N.A.T.O. Advanced Study Institute



LES SYSTÈMES SONARS ANIMAUX

Biologie et Bionique

ANIMAL SONAR SYSTEMS



Biology and Bionics

Tome I



Frascati, Italie

26 sept. - 3 oct. 1966

Édité par René-Guy BUSNEL

LABORATOIRE DE PHYSIOLOGIE ACOUSTIQUE

INRA - CNRZ - Jouy-en-Josas - 78

France


Avec l'aide financière de l'O.N.R., de l'U.S.A.F. et de l'E.O.A.R.

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réservés aux membres du Comité d'Organisation
et aux participants du colloque.
Exemplaire N°

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COMITÉ D'ORGANISATION
ORGANIZING COMMITTEE

R.-G. BUSNEL	Laboratoire de Physiologie Acoustique, C.N.R.Z. 78, Jouy-en-Josas - France
A. DZIEDZIC	Laboratoire de Physiologie Acoustique, C.N.R.Z. 78, Jouy-en-Josas - France
D. GRIFFIN	The Rockefeller University New York, N.Y. 10021 - USA
L. GERARDIN	Cie Française Thomson Houston, Groupements Systèmes Electroniques Radars 92, Bagneux - France
L. KAY	Department of Electrical Engineering, University of Canterbury Christchurch, 1 - New Zealand
W.N. KELLOGG	P.O.Box 551 Sarasota, Florida - USA
J.C. LEVY	E.N.S.A., Cité Fournier 78, Vélizy - Villacoublay - France
W. McLEAN	U.S. Naval Ordnance Test Station China Lake, California 93555 - USA
F.P. MÖHRES	Zoophysiologicalsches Institut, Universität Tübingen Tübingen - Germany
P. SABATHÉ	D.C.A.N., 8, Bd. Victor 75, Paris 15ème - France

SYMPOSIUM SUR LES SYSTÈMES SONARS ANIMAUX
SYMPOSIUM OF THE ANIMAL SONAR SYSTEM

LISTE DES PARTICIPANTS

CONFERENCIERS - LECTURERS

AUDOUIN (Francis)	Cie Française Thomson Houston, Groupements Systèmes Electroniques Radars 92, Bagneux - France
BASTIAN (Jarvis R.)	Department of Psychology, University of California Davis, California - USA
BATTEAU (Dwight W.)	College of Engineering, Dept. of Mechanical Engineering, Tufts University Medford, Massachusetts - USA
BUSNEL (René-Guy)	Laboratoire de Physiologie Acoustique, C.N.R.Z. 78, Jouy-en-Josas - France
CAHLANDER (David)	Control Data Corporation, Arden Hills Operations 4201 North Lexington, Arden Hills, Minn. - USA
CALDWELL (David K.)	Curator of Ichthology, Los Angeles County Museum Los Angeles, California 90007 - USA
CALDWELL (Melba)	Alan Hancock Foundation, UCLA Los Angeles, California - USA
DIJKGRAAF (Sven)	Laboratorium voor vergl. Fysiologie der Rijks- Universiteit Jan van Galenstraat 17, Utrecht - Netherlands
DZIEDZIC (Albin)	Laboratoire de Physiologie Acoustique, C.N.R.Z. 78, Jouy-en-Josas - France
EVANS (William)	U.S. Naval Ordnance Test Station China Lake, California - USA
FEDERICI (Maurizio)	Marconi Italiana via A. Negrone, Genova Cornigliano - Italy
GERARDIN (Lucien)	Cie Française Thomson Houston, Groupements Systèmes Electroniques Radars 92, Bagneux - France
GIBOIN (Eugène)	Scientific Affairs Division, N.A.T.O. Place du Maréchal de Lattre de Tassigny Paris 16e - France
GOURLAY (Paul)	D.C.A.N. Brest - France
GRIFFIN (Donald R.)	The Rockefeller University New York, N.Y. 10021 - USA

GRIFFITHS (John W.R.)	Department of Electronic and Electrical Engineering University of Birmingham Birmingham 15 - England
GRIMLEY (W.K.)	U.C.W.E. Portland, Dorset - England
GRINNELL (Alan D.)	Department of Zoology, U.C.L.A. Los Angeles, California 90024 - USA
HENSON (O'Dell W.)	Department of Anatomy, Yale University Medical School, New Haven, Connecticut - USA
JOHNSON (C. Scott)	U.S. Naval Ordnance Test Station China Lake, California - USA
KAY (Leslie)	Department of Electrical Engineering, University of Canterbury Christchurch, 1 - New Zealand
KENSHALO (Daniel R.)	Department of Psychology, Florida State University, Tallahassee, Florida - USA
LEONARD (J.A.)	Department of Psychology, University of Nottingham Nottingham - England
LEVY (J.C.)	E.N.S.A. Cité Fournier, 78, Vélizy-Villacoublay - France
KOHLER (I.)	Institut für Psychologie der Universität Innsbruck, Schopfstrasse 41, Innsbruck - Austria
MACKAY (R. Stuart)	University of California, Space Sciences Laboratory, Berkeley, California - USA
MERMOZ (Henri)	Laboratoire Détection Sous-Marine, 83, Le Brusc - France
MÖHRES (F.-P.)	Zoophysilogisches Institut, Universität Tübingen, Tübingen - Germany
NEUWEILER (Gerhard)	Zoophysilogisches Institut, Universität Tübingen, Tübingen - Germany
NICOLAS (J.L.)	Laboratoire Détection Sous-Marine, 83, Le Brusc - France
NORDMARK (Jan)	5 Bagvagen, Lidingo - Sweden
NORRIS (Kenneth)	Department of Zoology, U.C.L.A. Los Angeles 24, California - USA
PIMONOW (Léonid)	C.N.E.T. - 1-3, Avenue de la République, 92, Issy-les-Moulineaux - France

POULTER (Thomas)	Stanford Research Institute Menlo Park, California - USA
POWELL (Bill A.)	U.S. Naval Ordnance Test Station China Lake, California - USA
PURVES (Peter)	Department of Zoology, British Museum of Natural History Cromwell Road, London S.W. 7 - England
PYE (J.D.)	Zoology Department, University of London King's College Strand W.C. 2 - England
RICE (Charles E.)	Bio-Sonar Laboratories, Stanford Research Institute Menlo Park, California - USA
RISNESS (E.J.)	U.C.W.E. Portland, Dorset - England
RUSSELL (Linsay)	100 Memorial Drive Cambridge, Massachusetts - USA
SCHNITZLER (Hans-Ulrich)	Zoophysiologicalisches Institut, Universität Tübingen Tübingen - Germany
SCHUSTERMAN (Ronald)	Stanford Research Institute Menlo Park, California 94025 - USA
SUGA (Nobuo)	c/o Prof. Y. Katsuki, Medical School, Tokyo Medical and Dental University Yushima, Bunkyo-ku, Tokyo - Japan
WEBSTER (Frederic A.)	Sensory Systems Laboratory P.O. Box 5145, Tucson, Arizona - USA
WILSON (J. Patrick)	Department of Communications, University of Keele, Staffordshire - England

OBSERVATEURS - OBSERVERS

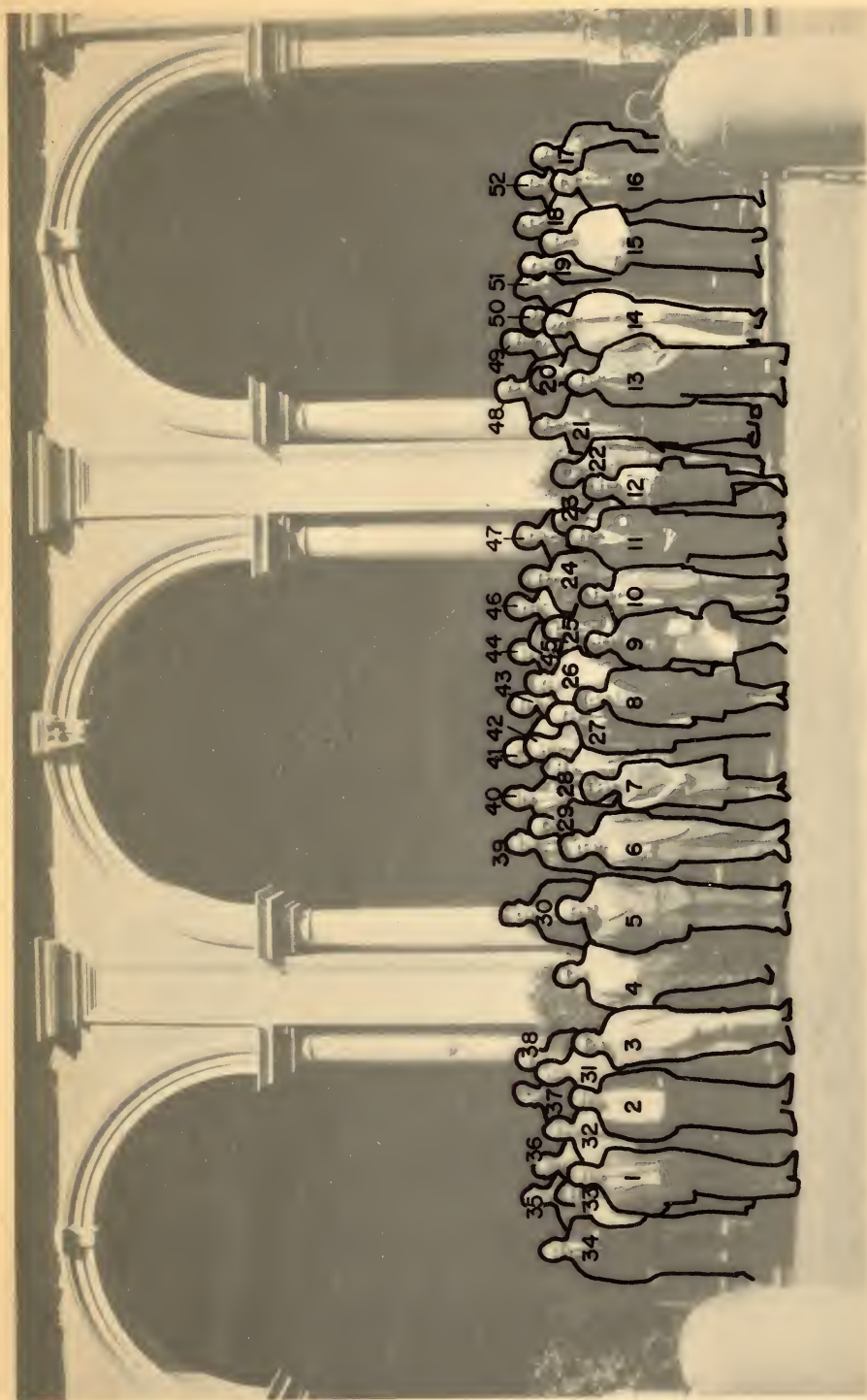
ANDERSEN (Søren)	Oceanographic Station "Anton Brun" Strib - Denmark
BANTLE (Herbert)	Zoophysiologicalisches Institut, Universität Tübingen, Tübingen - Germany
BARONE (Alfonso)	Istituto Nazionale di Ultracustica Pizzale delle Scienze 7, Rome - Italy

BUSNEL (M.C.)	Laboratoire de Physiologie Acoustique, C.N.R.Z. 78, Jouy-en-Josas - France
DAIFUKU (Alice)	Laboratoire de Physiologie Acoustique, C.N.R.Z. 78, Jouy-en-Josas - France
DIERCKS (K. Jerome)	Echo Structure Section, Acoustics Division, Defense Research Laboratory, University of Texas Austin, Texas - USA
FERRIEU (G.)	Centre National d'Etudes des Télécommunications Route de Trégastel, 22 Lannion - France
FOURNIER (Anny)	Laboratoire de Physiologie Acoustique, C.N.R.Z. 78, Jouy-en-Josas - France
FRAZER (F.C.)	Dept. of Zoology, British Museum of Natural History Cromwell Road, London S.W. 7 - England
HANFF (Michel)	Cie des Compteurs 12, Place des Etats-Unis, 92, Montrouge - France
HAYES (Helen)	Oceanic Biology Program (Code 408B), Office of Naval Research, Dept. of the Navy Washington, D.C. 20360 - USA
HERVIEU (R.)	Ecole Nationale de la Marine Marchande du Havre 76 Sainte-Adresse - France
HUFF (Lloyd C.)	US Navy Underwater Sound Laboratory Fort Trumbull, New London, Connecticut - USA
HUG (Edward)	Acoustics Research Division, Physics Research Dept. U.S.N.O.L., White Oak Silver Spring, Maryland - USA
JOSSERAND (Pierre)	Laboratoire d'Electroacoustique 2, rue Camichel, 31 Toulouse - France
MARX (Wolfgang)	Zoophysiologisches Institut, Universität Tübingen, Tübingen - Germany
MØHL (Bertl)	Oceanographic Station "Anton Brun" Strib - Denmark
MOLLOY (P.)	Dept. of Electrical Engineering, Lanchester College of Technology Coventry - England
MOREUIL (Andrée)	Laboratoire de Physiologie Acoustique, C.N.R.Z. 78, Jouy-en-Josas - France
NOVICK (Alvin)	Dept. of Biology, Yale University, New Haven, Connecticut - USA

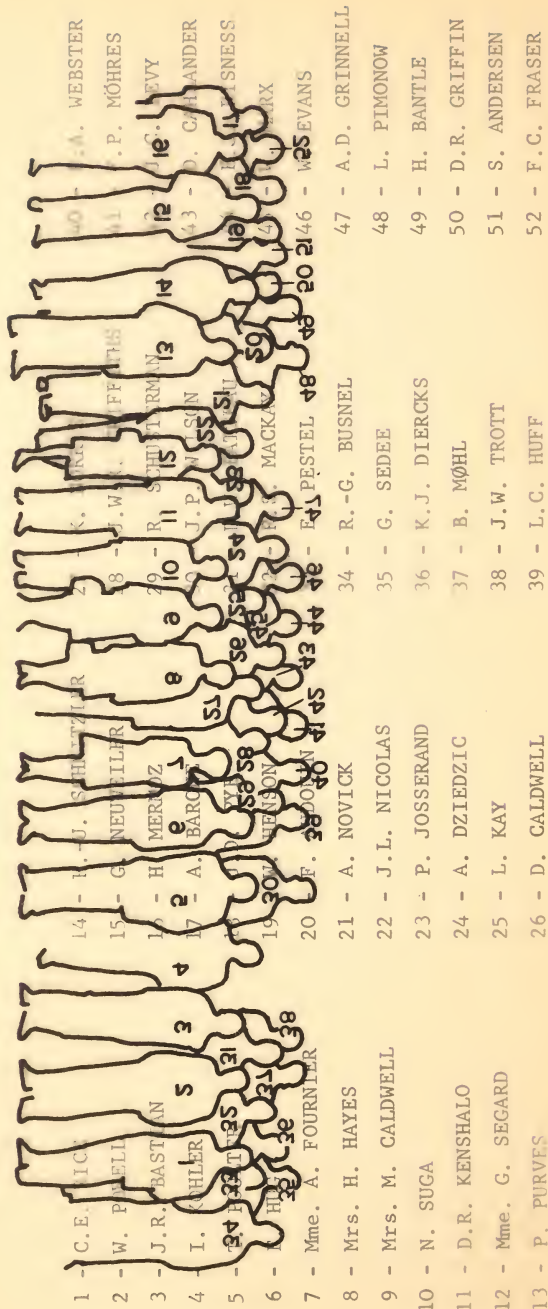
PESTEL (E.)	Lehrstuhl und Institut für Mechanik, Technische Hochschule Hannover Hannover - Germany
PESTEL (Robert)	Institut für theoretische Physik, Technische Hochschule Clausthal-Zellerfeld - Germany
PEYRAUD (Claude)	Laboratoire de Biologie Animale, Faculté des Sciences 38, rue des Trente-Six Ponts, 31 Toulouse - France
SAVELY (Harvey)	A.F.O.S.R. - 1400 Wilson Blvd. Arlington, Virginia - USA
SEDEE (Gilbert)	Wilhelmina Park 44 Utrecht - Holland
SEGARD (G.)	D.R.M.E. - 5 bis, Avenue de la Porte de Sèvres Paris - France
de SUSBIELLE (Geneviève)	93, rue de Prony Paris 17e - France
TROTT (James W.)	ONR, Keysign House 429 Oxford Street, London W. 1 - England
WODTKE (Monika)	Laboratoire de Physiologie Acoustique, C.N.R.Z. 78, Jouy-en-Josas - France
WOOD (Forrest G.)	U.S. Naval Ordnance Test Station, China Lake, California - USA

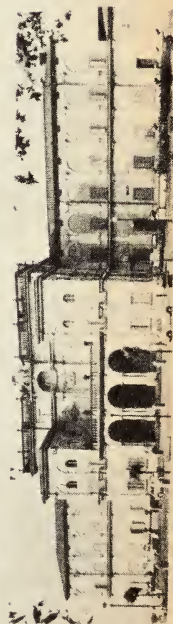
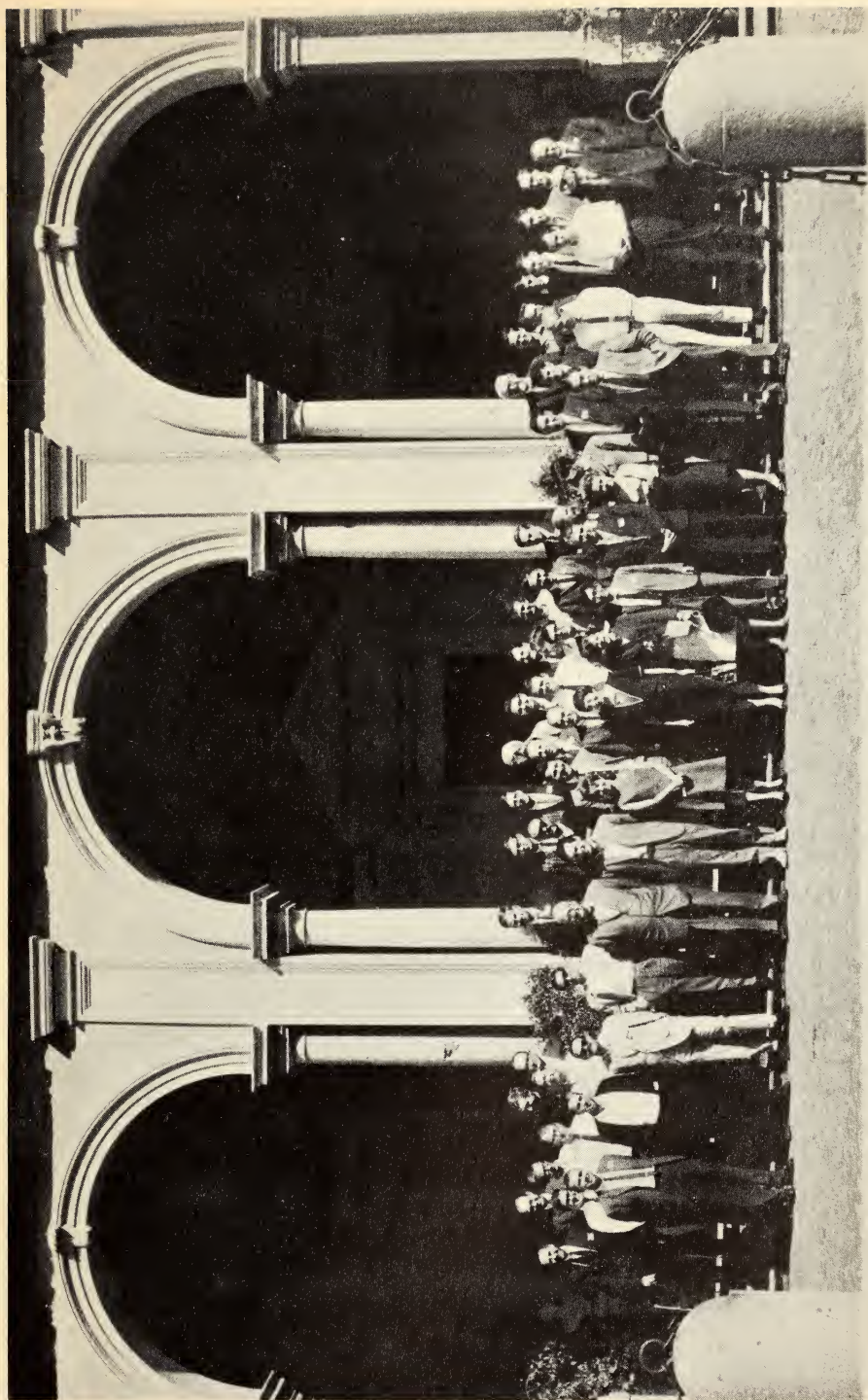
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INTRODUCTION

par

R.-G. BUSNEL

Le phénomène dit d'écholocalisation a été essentiellement l'oeuvre de biologistes, qui ont eu le privilège de le découvrir et de le mettre en évidence, à la suite de toute une série de brillantes démarches expérimentales; l'heuristique reconstituera un jour les approches successives qui forment, au cours de deux périodes séparées par près de deux siècles, une belle anthologie de l'évolution d'une pensée scientifique.

Les deux monographies modernes, "Listening in the dark" de Donald GRIFFIN et "Porpoise and Sonar" de Winthrop KELLOGG, forment la clef de voûte des documents de base qui ont porté à la connaissance d'une vaste audience l'essentiel des données acquises actuellement.

D'une manière tout à fait indépendante, depuis LANGEVIN, les physiciens et les ingénieurs, ont de leur côté, construit d'abord les théories de systèmes d'écholocalisation pour aboutir rapidement aux appareillages évolués que constituent sonars et radars.

On conçoit alors sans peine que, familiers de ces problèmes dont ils maîtrisaient les éléments nés de leurs entreprises et de leurs acquis techniques, ils aient leur attention particulièrement attirée par l'écholocalisation animale que leur révélait ces ouvrages, et qu'ils commencent de se préoccuper des appareils biologiques; d'autant plus que les performances, les énergies mises en jeu, les conditions d'utilisation, les informations reçues à partir d'un écho par les diverses machines animales sont dans l'état actuel de la technologie sans aucune mesure, et par beaucoup de points, infiniment supérieures, aux constructions humaines.

Ce serait à partir des données de la biologie que l'approche mathématique, l'analyse des signaux, l'usage méthodologique des ordinateurs, devraient

permettre aux spécialistes de la cybernétique et de la bionique de tenter d'aboutir à des principes les conduisant vers de nouveaux modèles perfectionnés.

On pourrait alors se demander si la somme des données biologiques déjà acquises est cohérente, et recouvre l'ensemble minimum à partir duquel l'extrapolation électromécanique de l'ingénieur, ou la théorie du physicien seront concevables et si les critères de choix des informations, nécessaires à ces disciplines, peuvent correspondre à celles définies ou obtenues par les biologistes. Faire le point de ces connaissances entre les biologistes, et répondre aux questions des ingénieurs et des physiciens était l'objectif majeur de la rencontre de FRASCATI, ce lieu ayant été choisi en hommage à la patrie de l'inventeur de l'écholocation, le prêtre italien Lazzaro SPALLANZANI (1729-1799).

Il est alors très vite apparu, et on en prendra conscience à la lecture, des discussions, qu'on se trouvait en présence de pensées très divergentes et que l'établissement d'une logique commune n'était pas toujours aisé.

En effet, déjà dans le seul domaine biologique, la pluralité des connaissances acquises est déjà considérable, les bioacousticiens ont conscience que le problème de l'écholocation est à multiples facettes; il est actuellement impensable de tendre vers une théorie unitaire, car, même pour les espèces aériennes et les espèces aquatiques, on observe pour une même finalité l'utilisation de principes physiques qui semblent différents, et dont les critères princeps même ne sont pas encore tous parfaitement connus. De plus, les différences d'attitude de pensée du physicien et surtout de l'ingénieur qui vit

dans un domaine relativement fini, et de celle des biologistes, est une source d'opposition entre deux concepts, celui de totalité organisatrice, et celui d'associations élémentaires, ou encore de deux attitudes de l'esprit foncièrement dissemblables, qui proposent deux classes de phénomènes, ceux d'ordre proche et ceux d'ordre lointain.

Le biologiste est un observateur, plus il se rapproche des éléments du système plus les microstructures de ces éléments lui apparaissent, au détriment d'une conception d'un ordre éventuel à grande échelle, qui se dissout dans les contingences particulières intéressantes pour son étude. Il oeuvre sur une matière infinie, qu'il ne peut entièrement embrasser.

L'ingénieur, qui veut s'appuyer sur les données de la biologie, les intègre dans un ordre lointain; il tend à n'en dégager que des régularités, des structures hiérarchiques, et oublie ou néglige les fluctuations locales ou particulières pour aboutir à une fonction globale, pour proposer une rationalité de l'architecture du phénomène. Ces deux tendances ne peuvent aboutir, passagèrement du moins, qu'à un conflit dialectique.

Le domaine de l'écholocation n'échappe pas à ces grandes règles des conduites scientifiques, c'est-à-dire que la recherche non seulement n'est pas monolithique, mais encore, que la trop grande spécialisation aboutit à la méconnaissance des thèmes connexes.

La dispersion obligatoire des intérêts et des techniques infiniment variées de la biologie, et la diversité des données expérimentales qui en découle, rend bien difficile déjà pour les seuls biologistes, de posséder une connaissance exhaustive des domaines limitrophes: a fortiori entre des mondes aussi éloignés que ceux des ingénieurs et des biologistes. Si même parfois des courants osmotiques de pensée

tendent à s'établir, la divergence babelienne des terminologies et des concepts d'approche des problèmes, tend vers un accroissement du taux ordre/désordre, c'est-à-dire vers une entropie négative grandissante.

La philosophie de la réunion dont les compte-rendus forment ce livre est basée sur ces contrastes humains; elle est celle d'un rêve du "possible" dans le sens de Paul VALÉRY. L'objectif était d'amener de tels groupes d'hommes à se rencontrer, à se connaître, et de les conduire à discuter, selon leur forme d'esprit, et leurs propres recherches, sur un thème qui se voulait commun.

Pour tendre à une unité de principe, les discussions ont été préparées plusieurs mois à l'avance, par écrit et par échange d'informations entre les participants. Ces entretiens mettaient en présence des unités de travail comprenant plusieurs disciplines: biologie, physique, mathématiques, science de l'ingénieur. Il était présumé l'établissement d'un vocabulaire commun, pour essayer de construire un système relativement unitaire.

Le lecteur pourra peut-être retrouver ce fil conducteur, tout au long de l'ouvrage, et jugera si le projet n'est pas trop ambitieux. Ce qui est certain, c'est que désormais des personnalités si différentes d'origine, de formation et d'intérêt, ont établi des contacts intellectuels et, de ce point de vue, la réunion aura atteint son but.

De ces confrontations, il ressort nettement que si on a beaucoup discuté biologie, physiologie et psychophysiologie sensorielle, la sphère de la bionique n'a été qu'effleurée; peut-être cet espoir était-il prématuré et nos méconnaissances actuelles ne permettaient-elles pas de l'aborder fructueusement.

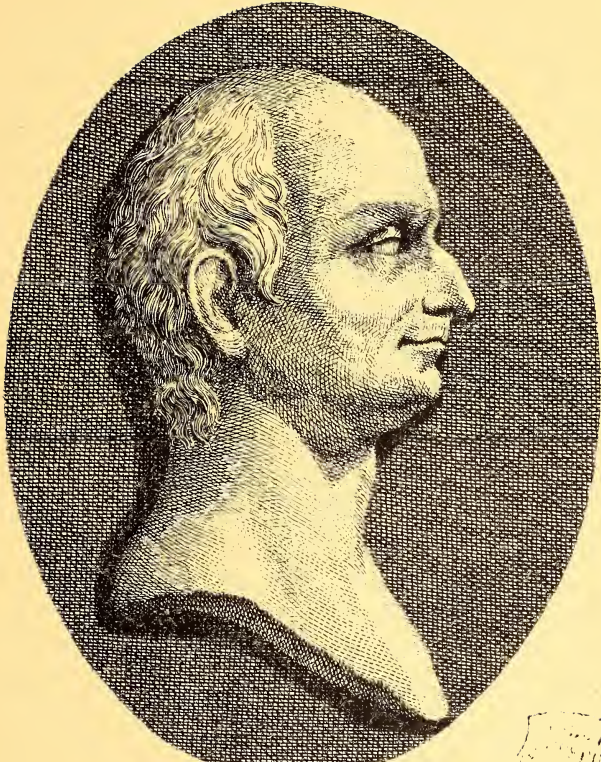
Ce livre constituera cependant, il faut l'espérer, un point de départ pour de nouvelles approches de ces fascinants problèmes, en vue d'une future émergence de systèmes et de théories, permettant d'aboutir, avec la maîtrise scientifique de ces fonctions, à des applications techniques nouvelles.

REMERCIEMENTS

Cette réunion n'a été possible qu'avec l'aide de nombreux organismes nationaux et internationaux, qui, à titre divers, ont apporté leur concours efficace. Ce sont :

- Le Bureau des Affaires Scientifiques de l'Organisation du Traité de l'Atlantique Nord
- L'Office de Recherches Navales de la Marine des Etats-Unis
- Les Forces Aériennes des Etats-Unis, European Office of Aerospace Research
- Le Ministère de l'Education Nationale du Gouvernement Italien
- Le Directeur et le personnel de la Villa Falconieri
- L'Institut National de la Recherche Agronomique du Gouvernement Français

Que tous ceux des membres de ces services qui ont personnellement contribué au succès du projet veuillent bien trouver ici l'expression de la vive reconnaissance du Comité d'Organisation du Colloque.



C. Neupoldt del. et inc.



Lazzaro Spallanzani

OPERE
DI
LAZZARO SPALLANZANI

Vol. IV.

S A G G I O

di osservazioni e sperienze intorno all'accecamento de' pipistrelli, comunicato dal sig. Pietro Rossi, pubblico professore della R. Università di Pisa, al professore Spallanzani ()*.

2 febbrajo 1794.

Nel dì secondo di febbrajo dell'anno 1794 alle ore dieci della mattina nel gabinetto d'insettologia del professore Pietro Rossi, il termometro indicando la temperatura dell'ambiente artefatta essere a gradi dodici sopra il gelo, presenti il Fisico sperimentatore, i professori Torrigiani e Manzi, il lettore Giambattista Gherardi, avvenne esattamente tutto quello che qui appresso si narra.

Di due pipistrelli comuni (*vespertilio, murinus*, Linn. Buffon *Hist. nat.* VIII, 113, t. 16) avuti letargici e assiderati, e da un lieve e blando tepore restituiti progressivamente al moto e alla vita, scelto il men vivace, e questo destinato al volo, si osservò correre instancabilmente per lunga ora nel vano della stanza colla medesima rapidità di movimento che usano i pipistrelli d'avere nei dì più caldi d'estate. Il giorno era sereno, e il luogo dell'esperimento illuminato da un vivacissimo sole; non per questo volava il pipistrello men rapido o men si-

(*) Queste sperienze furono parimente fatte ad istanza dell'abate Spallanzani.

curo; non per questo urtava nei muri laterali, o negli angoli cadenti della volta, o nell'ingombri più oscuri che occupavano di tratto in tratto il campo del suo volo. A luce dubbia e languidissima i suoi moti sono stati egualmente celeri e destri; così a stanza oscura e in tenebre assolute per noi. Abbiamo cioè indotto dal non aver mai un momento udito sospeso il suo volo, nè il suono del più picciolo urto, che in un luogo angusto, a volta echeggiante, avrebbe dovuto infallibilmente giungere a nostri orecchi. Abbiamo soltanto osservato quest'unica differenza nel passaggio rapido della notte alla luce, che all'improvviso tornar del giorno il volo del pipistrello si faceva più agitato, più inquieto, più vivo; le sue volte un poco più spesse, le vibrazioni, le mosse delle sue ali più frequenti, più preste; volte, giri o ritorni men ripetuti, ali meno scosse, meno vibrato, più lungo tempo tese in luce più languida, più modesta, talchè nessuna diversità nella sicurezza, nella rapidità del suo volo, solamente una qualche leggiera ma sensibile differenza nel modo di farlo.

Dopo ciò ci siamo volti all'altro pipistrello; lo abbiamo acciecato: Giambattista Gherardi, noi presenti, ha con un ferro adunco e finissimo tratti tutti i due bulbi degli occhi dalla loro cassa, che ha quindi divelti e tagliati al di là del nervo con una forbice; l'accecamento è infallibilmente seguito. Il pipistrello è ben presto risorto dal dolore di quest'operazione, ha preso il volo, volo rapido, sicuro, pieno di direzioni risolte, ardite, vivaci nè più nè meno

che il pipistrello veggente. Hanno ambedue lungamente volato, e al paragone non abbiamo saputo distinguere nei loro moti differenza veruna; sicchè abbiám finalmente confuso e smarrito col cieco il veggente, mancatoci l'indizio d'un picciol filo che avevamo stretto al piede del primo. Osservando che il cieco dirigeva i suoi voli verso un lato determinato di quella stanza più spesso che altrove, abbiám lì fatto sorgere all'improvviso una nuova inaspettata parete, distendendo un braccio lontana dal muro una rete da cacciare uccelli, di larghissime anella, e così abbiám inteso d'assicurarci ad un tempo che l'aria vibrata prima dalle sue ali, e quindi ripercossa dalla resistenza del muro, non fosse alla squisita sensibilità dell'ali sue di rapido e occulto avviso di cambiar direzione per evitare l'incontro dei corpi; ed in secondo luogo, per allontanare e distruggere il sospetto che i primi suoi voli per caso felici da quella parte gli avessero dato come il modo di far sicuri egualmente i secondi, e che si dovesse alla cieca abitudine celereamente formata, quel che noi avremmo attribuito al principio ignoto che lo guida e lo scorge felicemente, benchè cieco in tutti i suoi moti. Il nostro cieco non ha urtato mai nemmeno per disgrazia. Abbiám ad arte raddoppiato gli ingombri, abbiám colla rete diviso il campo del suo volo nelle più irregolari sezioni: una pianta di gorgonia avanzava pendente nel vano della stanza, una lumiera ne occupava il centro, l'area era come meandrica; a misura che è cresciuta la difficoltà del volo, si è raddoppiata la sa-

gacità di eseguirlo, e si può ben dire in verità che ai quattro veggenti non è stato possibile di far inciampar un cieco.

È avvenuto che volando abbia qualche volta oltrepassato la sommità della rete, e sia rimasto come imprigionato fra essa e il muro; la larghezza non era che un braccio, l'egresso era difficile e angusto ai lati e verso terra; noi l'abbiam più volte veduto uscire da questo carcere con una felicità che ci ha infinitamente sorpresi.

La stanchezza l'ha costretto alcuna volta a fermarsi; esso cadea sulla rete, ma senza precipizio e senza scontro, con un movimento per così dir preparato; ed era ben chiaro ad ognuno che il suo fermarsi non era urto inaspettato e improvviso, ma volontà di raccogliere le ali, bisogno di sospendere il volo.

Dopo un sì lungo esercizio la debolezza del pipistrello è aumentata, le rote del suo volo erano visibilmente languide e stanche, sicchè non potendosi più sostenere nell'alto, ha cominciato a piegare a terra il suo volo; ma è sembrato ch'esso abbia voluto impiegare l'ultime sue forze a far più luminoso e sicuro il risultato della nostra esperienza, poichè non permettendogli lo sfinimento di volare più in alto, nè il timore lasciandolo posare ancora, esso fuggiva terra terra passando velocemente e smarrito tra le gambe dei circostanti, tra i piedi dei tavolini (*), delle seggiole, d'un ca-

(*) È da osservarsi che la stanza degli esperimenti non era più lunga di braccia $9\frac{1}{2}$, nè più larga di braccia 6.

napè, evitando sempre ogni più piccolo urto d'alì o di corpo tra tanti prossimi pericoli, e quasi direi tra tante necessità d'inciampare.

3 gennajo suddetto: tempo sereno. Ore 11 della mattina.

Si sono rinnovate con i medesimi pipistrelli le medesime esperienze del giorno scorso, e non abbiamo osservata differenza alcuna nei risultati dei nuovi tentativi lungamente ripetuti alla presenza del professor Pignotti, dei soliti testimoni niuno mancando fuori che il sig. Torrigiani.

Il pipistrello ha eseguito coll'usata destrezza i suoi voli, ora lambendo quasi direi la terra, ed ora sorvolando le reti che nel vuoto della stanza si presentavano in più guise ad impedire la libertà de' suoi moti.

È unicamente da aggiugnersi che vedendolo noi scorrer per l'aria senza legge uniforme di moto, e tagliar col volo in ogni senso l'area della stanza, abbiám più volte improvvisamente offerto incontro al suo volo, già determinato e già steso, una spaziosa rete, che esso ogni volta ha con un nuovo moto come di pentimento evitata; e dopo aver così chiuso lungamente i suoi moti in uno spazio sensibilmente più angusto, gli abbiám tolto l'inciampo, ed esso si è gettato da quella parte, come se un senso visivo lo avesse rapidamente avvertito che l'impedimento era dileguato.

4 gennajo suddetto: tempo sereno. Ore 10 della mattina.

In questo giorno pure sono state dai professori Pietro Rossi e Tito Manzi ripetute nella

solita stanza e al solito ambiente con gli stessi pipistrelli presso a poco tutte le già fatte esperienze, ed altre ancora, alle quali han corrisposto sempre i medesimi risultati.

Prima però di passare ad esporre ciò che tentato oggi abbiamo di nuovo, non deesi più tralasciar di avvertire un picciolissimo fatto, che sempre accaduto nei passati esperimenti, si è rinnovato in quest'ultimo ancora.

Il pipistrello acciecato giunge spessissimo con i suoi voli fino al contatto del muro, ove sembra fermarsi un istante, come cercando coi piedi d'avanti e di dietro un appoggio che la parete sdruciolevole sempre gli nega, e ch'esso ritorna come per abitudine sempre inutilmente a cercare: questo avvicinamento estremo e frequente al muro, che non è urto, perchè comune ugualmente al veggente, dee far giungere il cieco nella corrente d'aria, che mossa prima dalle sue ali, rimbalza quindi dal muro contro di esso; ma sordo a quest'avviso, creduto comunemente l'occulto direttore del suo volo, pur segue di qualche linea ancora il cammino, mostrando che la sua nuova fuga nasce piuttosto da impossibilità conosciuta di progredire, che da un timore nato improvvisamente d'urtare. E pur da osservarsi che malgrado questa reazione d'aria, ivi certamente più che altrove maggiore, i suoi tentativi per cercar questo sostegno, nella nostra stanza sono stati sempre diretti al muro, ed ivi cercati, raramente, e quasi mai in qualunque altro corpo.

Avendo poi primieramente ripiene le casse degli occhi del pipistrello d'una materia seba-

cea e viscosa, più per diminuire gli altrui sospetti che per accrescere la sua cecità, esso ha volato senza urto in mezzo ai soliti ostacoli della stanza: gli abbiamo quindi spalmata e introdotta anche della stessa materia nelle narici, e nuovamente lasciato, le sue fughe sono state all'ordinario rapide e sicure.

Sempre più sorpresi e sempre più avidi del segreto, volendo escludere il dubbio della possibilità di vedere per mezzo di qualunque altro organo situato in tutta la regione del capo, siamo passati a poter facilmente rinchiudere la sua testa al di là del collo in un cartoccino di finissima carta sparsa di colla in sui lembi e convenientemente forato; ma secondo ciò che indotto dalla pratica in casi simili avea ben predetto il professore Pietro Rossi, tutto è stato inutile per muoverlo al volo, e scagliato in aria, apriva, cadendo, le ali per diminuire il colpo della caduta, e non più.

Si è finalmente voluto vedere se i suoi passi erano sicuri come il suo volo. Costruito sopra un piano un piccolo laberinto di vie tortuose, noi abbiamo veduto il pipistrello più frequentemente cercarne l'uscita, arrampicandosi alle pareti; ma costretto da noi di seguire il corso, esso volgeva agli angoli della sua prigione con una tal mossa preveduta e sicura, come se fosse stato veggente. Quest'ultimo tentativo però non ci è sembrato abbastanza decisivo, e merita d'essere rifatto.

6 gennajo suddetto: tempo assai freddo e nuvoloso. Ore 12 della mattina.

In questo giorno ci fu permesso dalla cor-

tesia del sig. professor Giorgio Santi di costruire nel giardino botanico di Pisa un piccol chiuso di reti all'aria aperta; noi lo facemmo di sei braccia lungo, largo di cinque, alto di quattro. L'oggetto di questo sperimento era, non avendo modo di toglierla affatto, di ridurre al *momento* più tenue di forza la ripercussione aerea delle pareti; dal cielo della rete pendevano fino a terra in sì picciol vuoto sedici fili di spago a guisa di colonnette separate quasi a *quincunce*, le quali, a dir vero, troppo poco intervallo avean tra di loro. Desti a fatica a un volo non molto vivace i due pipistrelli, il cieco e il veggente urtavano ugualmente nei fili, ambedue però colla punta estrema dell'ali; incontro nessuno mai del loro muso o del corpo; osservazione concorde di molti spettatori che onoravano di loro presenza l'esperimento, e dubbiosi tutti se l'urto nei fili era fatto inevitabile dalla loro spessezza e dall'angustie estreme del loco, più che da altro motivo: cielo freddissimo, luce di giorno cadente, sicchè per il pipistrello illuminato ed urtante al pari del cieco, ora del volar più sicuro. Frattanto il cieco per le radissime anella della rete fuggì, volò molto in alto, e lungo tempo dentro l'area del giardino; errò qualche momento, e quasi circondò col suo volo un altissimo capannone di cipressi senza posare; piegò finalmente con una fuga precipitosa e gradatamente inclinante verso il tetto più vicino ed unico del luogo, ove lo perdemmo di vista.

7 gennajo suddetto: tempo freddo e nuvoloso. Ore 12 della mattina.

Abbiamo ripetuto l'esperimento con i fili di spago dalla volta d'una stanza cadenti verso la terra, ed hanno urtato egualmente l'illuminato ed il cieco; se deesi chiamar urto il leggier tocco dell'estremo dell'ali, o impossibilità piuttosto di prender, fuggendo, la giusta misura d'espanderle ora più ed ora meno, secondo le angustie dei passi. Fatto sta che la loro testa che fugge nel volo in avanti assai più d'alcun'altra parte del loro corpo, e che dovrebbe esser la prima e la più facilmente percossa dagli ostacoli del cammino, non ha in tanti rinnovati cimenti urtato una sola volta ancora. Abbiamo all'incontro in mille occasioni osservato che giunto il cieco vicinissimo al corpo contro cui dee inevitabilmente urtar proseguendo, all'improvviso devia, poco sollecito della percossa e dello scontro dell'ali; due fatti che moveano l'animo del sig. professor Pietro Paoli presente a creder che le ali del pipistrello non sono nè sì delicate nè sì dolorose com'era pensiero d'alcuni, e che la sede della di lui sensibilità fosse, piuttosto che in altra parte, da riporsi nella regione intera del capo.

9 gennajo suddetto. Ore 10 della mattina.

Ci siamo adunque volti a dileguar questo sospetto, o a convertirlo in certezza: abbiamo di varj ingonbri leggierissimi, delicati e cedenti in varie guise vestito l'intero capo del pipistrello, che tutto inteso a togliersi con ogni maniera di sforzo da quest'inviluppo, ha reso tutti i nostri nuovi tentativi inutili, come i passati, per muoverlo al volo.

Morto forse per cagion degli sperimenti di languore e di stanchezza uno dei nostri ciechi volatori, il professore Pietro Rossi ha voluto che quello su cui non poteano più cadere le nostre sperienze, ci fosse mezzo a tentarne delle più sicure su gli altri già avuti, ed ha costruito con l'ala del morto pipistrello una benda al capo d'un vivo acciecato del giorno innanzi, che senza troppo infastidirlo e impedirgli la libertà del volare gli togliea sicuramente insieme coll'effetto della ripercussione dell'aria l'esercizio di quell'organo che guidava il suo volo, se mai la natura glielo avesse diffuso in tutta, o collocato in qualche parte della regione del capo. Il volo infatti già franco del nostro cieco è diventato sensibilmente men rapido; le vibrazioni delle sue ali moltissimo più frequenti; le volte più uniformi e men tortuose; è finalmente caduto più volte a terra, urtando con vero cozzo ora negli usci, ora nelle muraglie, e alcuna volta fino nella corda della lumiera sospesa nel mezzo della stanza, fra tanti voli innumerabili intorno ad essa, primo ed unico esempio. Pauroso forse del colpo, non si è veduto avvicinarsi mai più alle pareti, come son soliti ogni momento di fare tutti i pipistrelli o ciechi o veggenti. La benda è apparsa fare quel che gli occhi perduti non avevano fatto; sicchè lasciato al volo un altro pipistrello cieco; ma non bendato, la differenza è sembrata fra i due grandissima in tutto; e tolta nuovamente al pipistrello acciecato questa buffa cadentegli di qualche linea sotto il muso, è sembrato che noi gli abbiamo ridonato colla

vista la primiera sicurezza e agilità de' suoi voli.

Ore 3 pomeridiane: tempo nuvoloso.

Un avvenimento di tanta importanza non potea far a meno di non richiamarci alla stessa sperienza nel dopo pranzo; ed avendo cambiata la nera ala del pipistrello in una benda di bianchissima carta, fermata sul dorso dietro il capo dell'animale con cera di Spagna, lo abbiamo immantinente ricondotto agli urti, ai moti più timidi, più lenti, e a tutti i risultati della precedente esperienza.

Lo stesso pure è accaduto ad un pipistrello veggente (*), che in simil foggia bendato, non

(*) *Nota del professore Spallanzani.* Oltre alla compiacenza ch'io provo nel vedere che la massima parte dei fatti esposti in questo Saggio dal dottissimo e celebre sig. professore Pietro Rossi, si accorda perfettamente con quelli ch'io narro nella mia Memoria manuscritta trasmessa li 28 settembre scaduto all'illustre sig. Senebier di Ginevra, e che tuttora trovasi nelle sue mani, godo grandemente di essermi pure incontrato con lui nell'ultimo di questi fatti. Così adunque in essa Memoria io mi esprimo. *Avvisai con un cappuccetto di pelle nera ed opaca di imbacuccare alcuni pipistrelli veggenti. Pareva che allora dessero manifeste prove di più non vederci, poichè di rado si levavano di terra, e se pur si levavano andavano di colpo a percuotere le pareti della stanza; poi precipitavano sul suolo.*

Pago di queste osservazioni, più allora nulla pensai a siffatte curiose ricerche; solamente alcuni giorni appresso torndto essendo, non so come, col pensiero al cappuccio opaco onde io bendava i pipistrelli, mi venne talento di surrogarne un altro di tela rara, attraverso della quale io tollerabilmente discerneva gli oggetti, persuaso ch'eglino molto più potessero discer-

NEI PIPISTRELLI

meno degli altri l'abbiam veduto decisamente urtare nel muro, negli uscì e fino su di noi stessi.

ARTICOLO

di lettera intorno ai pipistrelli scritta dal signor Senebier, bibliotecario della Repubblica di Ginevra, al professore Spallanzani.

Genève, ce 25 janvier 1794.

J'ai lû à notre Société d'histoire naturelle votre mémoire sur les chauve-souris: il a excité tout l'étonnement qu'il devoit produire; je lui peignis le désir que vous avez qu'on répéta ces expériences, et chacun l'avoit; je lui appris les moyens de les répéter avec les chauve-souris qu'on pourroit avoir en les réchauffant. Monsieur Jurine, chirurgien, grand insectologue-ornithologue-botaniste, me promit de s'occuper de cela: il le fit dès le lendemain, et il trouva 17 chauve-souris dans les mines de nos fortifications, entre les quelles étoient l'oreiller, le grand et le petit fer-à-cheval. Il les réchauffa, il fit vos expériences après en avoir aveuglé quelques unes, et les expériences ont parfaitement réussi; il nous les a fait voir à une de

nerli; e l'esperimento si fece in picco giorno. Posti in una camera spaziosa, qualche fiata, è vero, volavano in modo che mostravano di valersi della potenza visiva, ma il più frequente urtavano contro le mura glie, come ciechi, e cadevano a terra senza più sollevarsi.

LETT. SU DI UN NUOVO SENSO NEI PIPISTRELLI
nos assemblées, et il doit dans le mois prochain nous donner un mémoire sur ce sujet. J'ai vu les chauve-souris aveuglées, qui vivoient 15 jours après l'opération, et qui voloient après avoir été réchauffées. Quand il nous aura lû son mémoire, je vous en ferai part. Notre Société me charge de vous remercier de cette communication.

I

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Free papers

SYNTHESIZING THE WAVEFORMS OF BAT'S PULSES

by

J. D. PYE

Over a number of years, Griffin and Novick (5, 9-12) have published oscillograph pictures of the orientation pulses from a wide variety of bats. Several features of the various waveforms were intriguing, for they had no ready explanation. Some of them are listed below:

1. Components of different frequency show marked changes in relative phase during frequency sweeps so that their harmonic relationships were in some doubt. Such phase shifts are not shown as long as the frequency remains constant within a pulse, but they often change appreciably between successive pulses in a train of such pulses.
2. The relative amplitudes of such components may vary rapidly within single pulses, but again only during frequency sweeps. These changes lead to strange pulse-envelope shapes which may, for instance, show two clearly separated peaks.
3. The envelope often shows amplitude modulations, either at a sub-multiple of the carrier frequency or, in other examples, at other lower frequencies.
4. Many of the waveforms represent almost pure notes of sinusoidal form which are perhaps more remarkable than a series of harmonically related components and suggest that they are derived from a tuned system.

During the last two years I have collected recordings on magnetic tape of the ultrasonic pulses produced by over 65 species from all the 13 major families of the Chiroptera (the other four families are either rare,

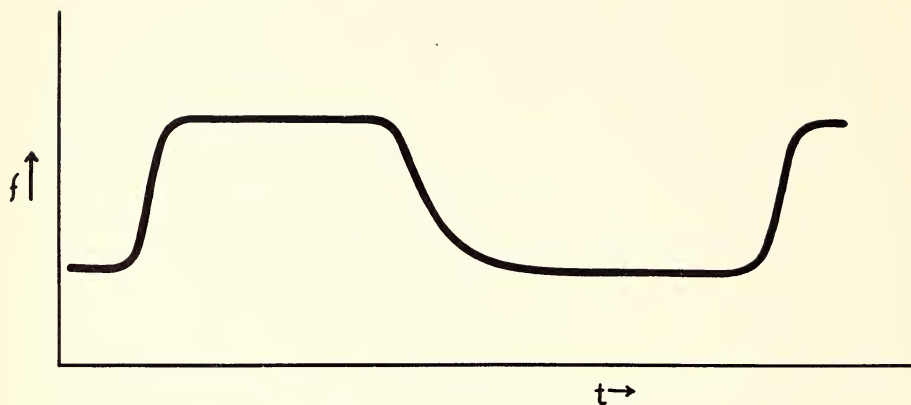


Fig. 1. A composite frequency-time pattern from which all bat pulses can be derived.

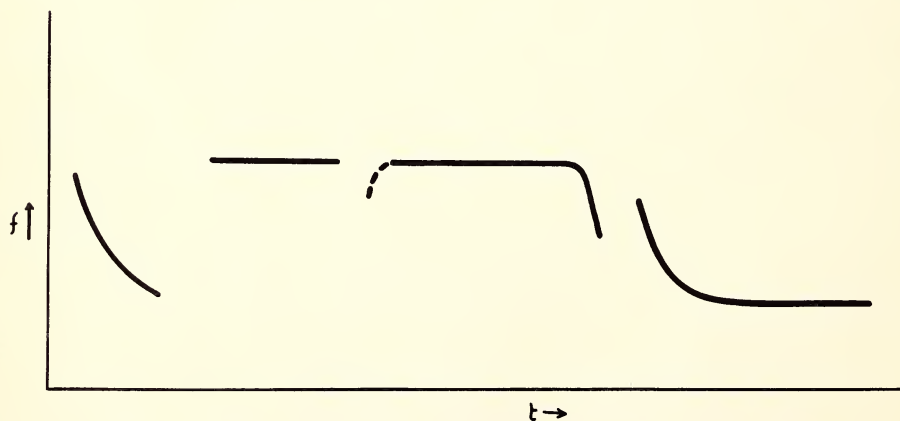


Fig. 2. Four characteristic frequency-time patterns for bat pulses: (a) frequency sweep; (b) constant frequency; (c) and (d) two possible combined types.

some almost to the point of extinction, or have restricted distribution). These have been analysed by a method which combines for each individual pulse a spectrographic analysis of frequency (a Sonagram) with oscillographic examination of waveform and phase. The work has confirmed the above features, but has also shown that all the variations in pulse structure are continuous. This suggests that they are derived from a single basic pattern and that the mechanisms which generate them have much in common.

All the frequency patterns can be derived from a single curve (Fig. 1) by gating various sections. There are four main patterns - a frequency sweep, a constant frequency, and two combinations of these (Fig. 2).

Within each of these types the energy may either be distributed between a number of harmonic components, in which the fundamental and even the second harmonic may be suppressed, or be largely restricted to a single component which is not always the fundamental. Spectrographic analysis always confirms, within the limits of its accuracy, the harmonic relation of multiple components, and so far has not suggested that two or more harmonic series can exist.

The problems listed now require some explanation. First one should examine all the factors that can modify the waveform externally - i.e. from the time of emission by the bat to the final display. These fall into four categories:

(1) Effects introduced by the recording apparatus. Frequency response curves are usually supplied with commercial instruments and are easily measured for equipment constructed in the laboratory. But phase responses are much more difficult to determine. v.Gierke and v.Wittern (4) have

shown that the 640-AA capacitance microphone has a complex phase response, especially at higher frequencies. Further phase changes occur at every subsequent stage of the apparatus and are often frequency dependent. It is not safe even to assume that an amplifier with a 'flat' frequency response is beyond reproach. An inductance-capacitance band-pass filter gives a phase response of $+\pi$ to $-\pi$ (a total of 360°) between the limits of its flat frequency response (see 6, for example). Even resistance-capacitance filters, which represent the usual type of recording amplifier, give $\pm 45^\circ$ at the 3dB points. The amplified pulses may then be recorded on tape and reproduced at lower speed, perhaps more than once, before finally being displayed on an oscilloscope or Sonagraph.

The actual equipment used here has been described previously (14). Its frequency response was always 'flat' to at least 100 kHz and although the phase response has not actually been measured for any part of the equipment, the overall response has been observed as follows. A variety of imitation bat-pulse waveforms was produced as described below, radiated from an ionophone transducer and treated in exactly the same way as original bat signals. After passing through the analysing system the waveform was compared directly with that of the original pulse. Besides a reduction in signal/noise the differences between the waveforms were noticeable but quite inadequate to account for the effects listed above.

(2) Effects due to atmospheric propagation. Higher frequencies in the bat spectrum are absorbed quite rapidly in air. Figures given by Beranek (1) show that the attenuation in decibels is almost proportional to frequency (Table 1).

TABLE 1

frequency (kHz)	loss per m (-dB)	amplitude loss factor	intensity loss factor
30	1	0.89	0.79
84	3	0.71	0.50
158	6	0.50	0.25
200	9	0.35	0.12

This effect will be particularly important when broad-band signals are recorded out of doors from free flying animals which may be some distance from the microphone.

Pierce (13) also showed that there is some dispersion at ultrasonic frequencies. Although his results may be open to some doubt, there is little alternative information on the properties of crude air with water vapour and carbon dioxide included. Pierce's data for air at 0°C, interpolated to convenient figures, may therefore be taken to indicate the kind of effect expected (Table 2).

TABLE 2

frequency (kHz)	velocity (m/s)	path difference (mm) after 1 ms
22.5	332.27	0.17
45	332.44 (max)	0.0
90	331.86	0.58
180	331.68	0.76

Under these conditions a second harmonic of 90 kHz would be retarded in phase, relative to a fixed point-in-phase of its fundamental at 45 kHz, by about 170° for every metre travelled. It must be admitted that tests in the laboratory by transmitting this pair of frequencies along an optical

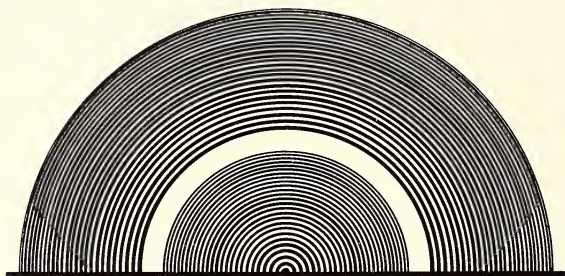
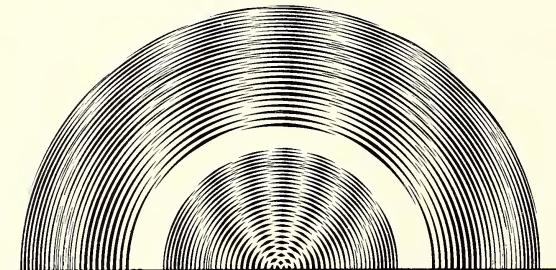


Fig. 3(a) Inner circles represent waves of a pulse, frequency modulated by one octave, emerging from a small aperture in a baffle.



(b) When two copies of Fig. 3(a) are superimposed, with a slight lateral displacement, the moiré pattern represents the interference effects produced by two sources. It is clear that the 'beams' rotate laterally as the frequency falls.

bench have so far failed to demonstrate the effect. But the point remains that very slight dispersion, if present, could have a marked effect on waveforms recorded at varying distance.

(3) Effects due to multiple pathways in air. When either a bat producing frequency-sweep pulses or the microphone is held near to a solid surface, an echo is also recorded after a slight additional delay. This produces beats or apparent amplitude modulation of the waveform. The presence of such beats can usually be predicted from a double sweep resolved on the Sonagram even before the waveform is examined (or vice-versa). In order to avoid this effect it is necessary to arrange that no alternative path shorter than one pulse-length is present. This is not always possible for the longer pulses and the effect is always marked for bats recorded while flying over water, e.g. Noctilio leporinus or Myotis daubentoni.

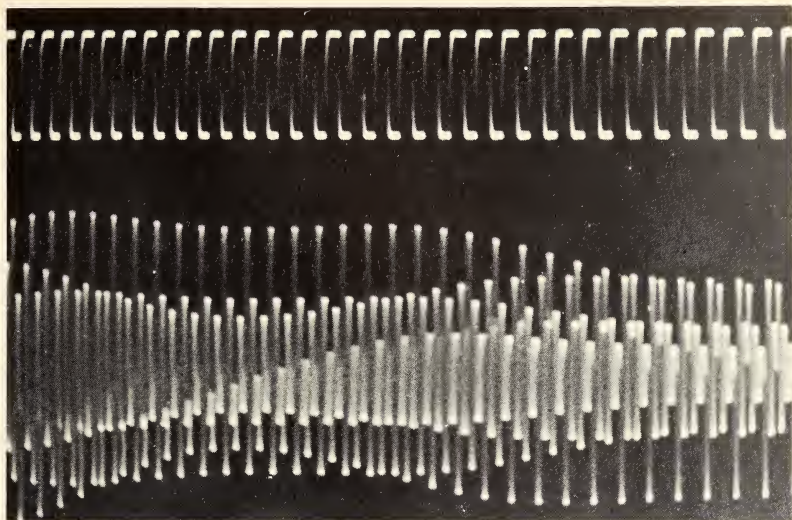
Even the constant frequency bats are not free from this effect. The amplitude modulation first noticed by M8hres (7) for Rhinolophus ferrumequinum when flying but not when at rest can be confirmed for a number of similar forms. It can be attributed entirely to the reception of Doppler shifted echoes from walls and other objects, and at close range even to standing waves between bat and microphone. These phenomena are easily reproduced by radiating artificial signals from a small movable transducer.

(4) Effects due to radiation patterns around the animal. Any emitter whose dimensions are comparable with the wavelength of its signal will produce a radiation pattern that is frequency dependent. The form of broad-band or multiple component signals thus depends on the relative

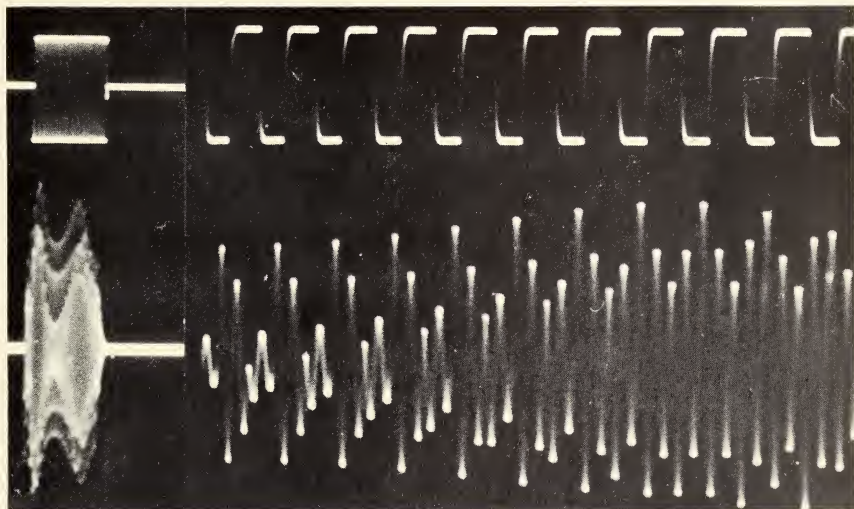
position of the microphone. This property is not easily defined for the bats which emit orally because the mouth is a complex and variable shape. For nose-leaf bats with nasal emission the situation is somewhat simpler and the effect more marked. Møhrhres (7) first pointed out that for several species of Rhinolophus the spacing between the nostrils closely approximates to half a wavelength of their constant-frequency, single component signal. This can be confirmed for a number of Rhinolophids and Hipposiderids between 45 kHz and 150 kHz. The interference pattern in two dimensions is easily constructed geometrically.

A more interesting case is presented by the Phyllostomatid bats which radiate a multiple-harmonic frequency-sweep from a nose-leaf. Here the pattern is different for each component and each pattern must change, by 'opening out sideways', as the frequency falls. The various patterns can be visualised by drawing concentric circles to represent a frequency modulated train of waves and superimposing two transparent copies to obtain a moiré fringe pattern. The relative lateral displacement of these can then be set in turn to represent the pattern produced by each component of a real pulse. It can be seen that microphone position must influence the structure (both the relative amplitudes and the phases of the components) of the recorded waveform in quite a complex way. For the higher components one may even get maxima or null-minima sweeping past the recording point during a single short pulse.

Such geometrical methods are an oversimplification, for they assume that the nose-leaf consists of two point sources in a plane baffle of infinite size. A more realistic situation has therefore been tested by



(a) Taphozous melanopogon (9). Frequency sweep and low Q give a complex waveform.



(b) Desmodus rotundus (5). Frequency sweep and 'high' Q can give a doubled-peak pulse (2nd harmonic followed by 3rd).

Fig. 4. Pulse waveforms produced electrically (lower traces) by passing a square wave (upper traces) through a fixed resonant filter. The model has here been set to give frank imitations of bat pulses published by Griffin and Novick (5, 9).

a simple physical model. Two holes of 3 mm diameter were drilled in a metal plate with 5.5 mm ($\frac{\lambda}{2}$ for 30 kHz) between their centres. A mixed signal of 30 kHz, 60 kHz and 90 kHz was then produced by an ionophone transducer, the tube of which was tightly sealed to one side of the plate. With the microphone 'straight ahead', normal to the plate, all three components were recorded. Then the microphone was placed in the plane of the plate on a line joining the hole-centres; the fundamental (30 kHz, $\frac{\lambda}{2}$) and the third harmonic (90 kHz, $\frac{3\lambda}{2}$) were now almost completely suppressed leaving only the second harmonic (60 kHz, λ). The differences in waveform were confirmed by a 'frequency section' analysis on a Sonagraph. This is still an oversimplification of the real case however, because nose-leaves have a very varied fine structure which cannot be explained at present. Some bats may also be able to influence the vertical pattern of sound emission or to make small but effective changes in nostril spacing.

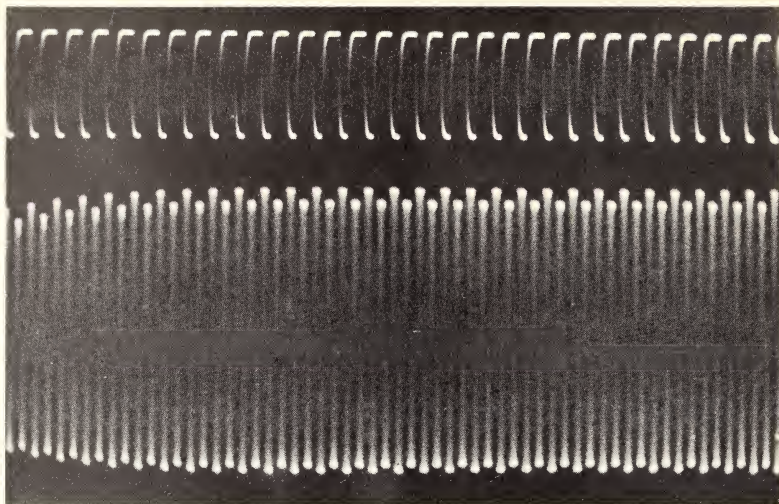
When all these external factors are taken into account, they are still insufficient to explain most of the initial phenomena, which must therefore be due to processes occurring within the bat itself. A feasible explanation of them has been found quite by accident. In order to examine the properties of echoes from bat-like pulses, an oscillator was 100% amplitude modulated by a square pulse and at the same time frequency modulated by a downward sweep as in Fig. 2. For convenience a square-wave multivibrator was used as the oscillator and an attempt was made to 'refine' its waveform by suppressing the harmonics with a tuned filter. The surprising result was that a variety of bat-pulse waveforms

appeared on the monitoring oscilloscope screen, including many of the puzzling features.

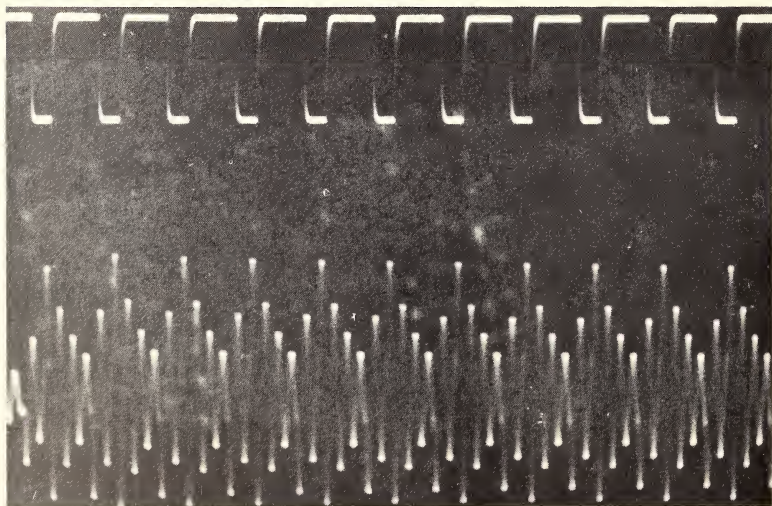
A general theory arising from this runs as follows. The laryngeal or glottal waveform in all bats is non-sinusoidal and contains a number of harmonic components although the spectrum may vary in different species. But before emerging into the outside world these signals must traverse the vocal tracts where they are influenced by the acoustic properties of the air-filled cavities. Passive resonances will then alter both the relative phases and amplitudes of the components and will lead to rapid changes of these during frequency sweeps.

This is after all precisely the phonetic theory of human vowel production (2, 3) where the glottal waveform is pulsed with harmonics decreasing at the rate of about 12 dB/octave, and there are four main resonant peaks, the formants. These formants have variable centre frequencies which may lie as high as the 30th. harmonic and together they fully define the nature of the vowel sound emitted. In the case of bats it is only necessary to postulate a single formant which is relatively much lower in the harmonic series, from the fundamental to the 4th or 5th harmonic. In cases of oral emission we may expect a broadly tuned resonance capable of changing under different conditions. For nasal emission through a nose-leaf, the epiglottis commonly, if not always, engages the internal nares so that the nasal cavity alone is effective and the resonant properties must be more rigidly defined.

These conclusions are well supported by a re-evaluation of recorded pulses, which will now be summarised. On this basis all the pulses may



(c) Rhinolophus landeri (9). Constant frequency and 'high' Q can give almost pure 2nd harmonic.



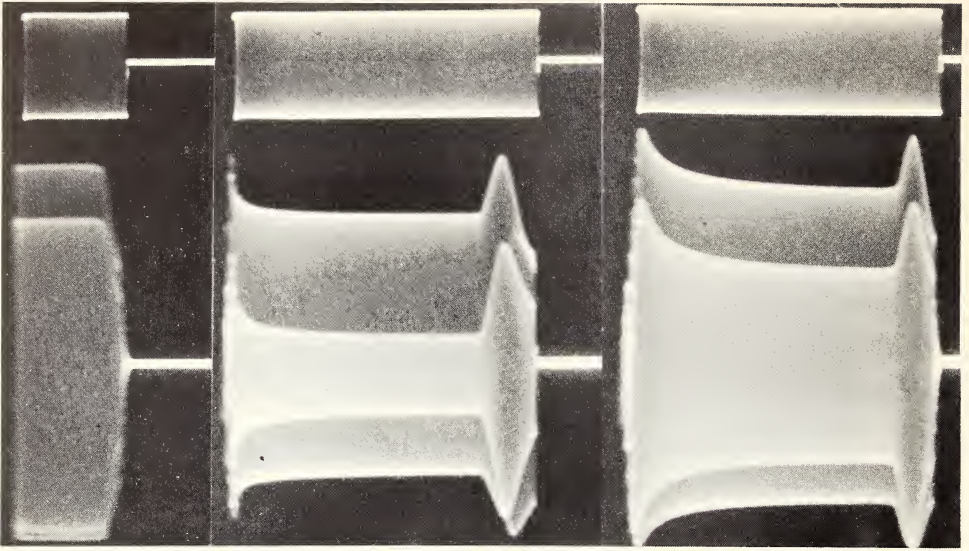
(d) Lonchophylla robusta (5). A 'high' Q selection of higher harmonics can give the appearance of amplitude modulation at a submultiple frequency.

be divided into five classes:

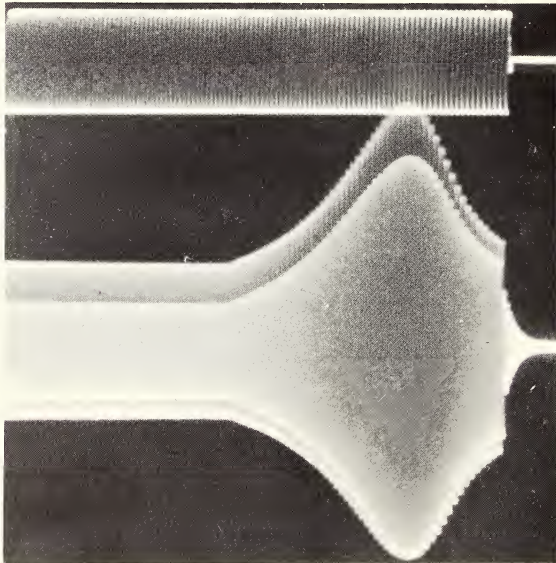
(1) Rousettus type. This genus is so far unique among the Megachiroptera in being able to orientate by acoustic signals. Möhres and Kulzer (8) have shown that pulses are produced in pairs by clicking the tongue, first on one side and then on the other. These signals are clearly audible to man, although an appreciable part of their energy is ultrasonic. Their envelope shape is that of a shock-excited resonator with a sharp rise-time and more gradual decay. Clearly the mouth or cheek cavities could act singly or together to produce this effect. It is easily imitated by the human mouth which can be excited in a number of ways and tuned as in whistling a melody.

(2) Vespertilionid type. Most species produce a frequency sweep of short duration (Fig. 2a) although when hunting out of doors some species such as Pipistrellus pipistrellus prolong the pulse into the lower constant-frequency region (Fig. 2d) and Nyctalus noctula may eliminate the sweep entirely. Emission is oral except in Plecotus and possibly in Barbastella. The fundamental predominates, especially in Myotis although even there the 2nd harmonic can usually be detected at appreciable amplitude towards the end of the pulse. In some forms, for example Plecotus and Nyctalus, the 2nd harmonic and even the 3rd harmonic are often very marked. Eptesicus serotinus produces extremely variable pulses, sometimes with the first four harmonics all at high intensity.

In all species during special manoeuvres the pulse repetition rate is increased to very high values ($100-200\text{s}^{-1}$), the pulse is shortened, the frequency sweep is restricted and lowered and the harmonic content is increased. The whole picture suggests a low Q filter with rather variable resonant frequency coupled to a relatively pure or perhaps variable glottal waveform.



(a) Rhynchiscus naso (5). Three pulses showing changes in the envelopes produced by slight frequency shifts.



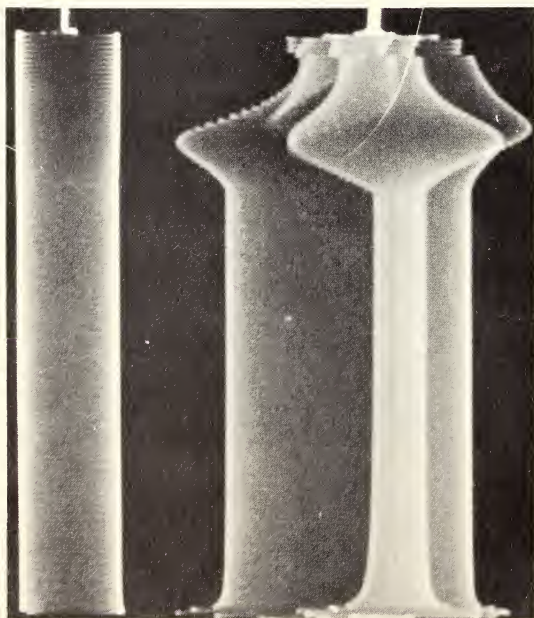
(b) Rhynchiscus naso (5). The end of a pulse at higher time-base speed to show a peak produced by a terminal frequency sweep.

Fig. 5. Pulse envelopes produced by the electrical model in imitation of bat pulses published by Griffin and Novick (5, 11, 12).

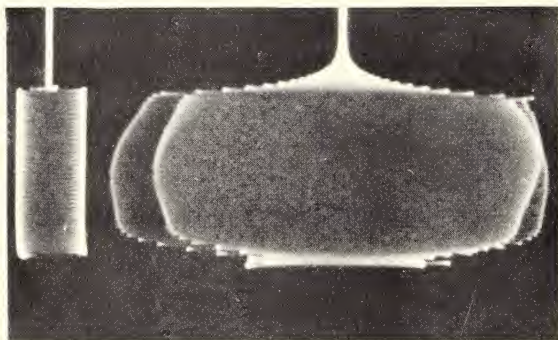
(3) Phyllostomatid type. Apart from the Chilonycterines, the majority of species in this family and several other families again produce a short frequency sweep, but it is emitted nasally through a nose-leaf. There are several harmonics, of which two are sometimes accentuated in turn to give double-peaked pulse envelopes. The sequence might be as follows: The fundamental is suppressed or fades rapidly, the 2nd harmonic provides the initial peak but is replaced by the 3rd harmonic which produces the second peak. The 4th, 5th and even the 6th harmonics may appear later as the frequency falls, but they are often faint and detectable only in the Sonagram. Relative phase shifts are especially prominent in the waveform as one harmonic fades and is replaced by another.

Even during manoeuvres when the pulse rate rises, the formant structure does not vary appreciably. During the selection of higher harmonics the waveform shows 'amplitude modulation', independently of echo effects, at a sub-multiple of the 'carrier frequency'. That is, there are amplitude maxima every 3rd, 4th or 5th cycle of the predominant component. This is typical of a mixture of sinusoids at the appropriate frequencies, as can be checked with two oscillators and an oscilloscope. In the present case it indicates a relatively high Q resonator with narrow tuning.

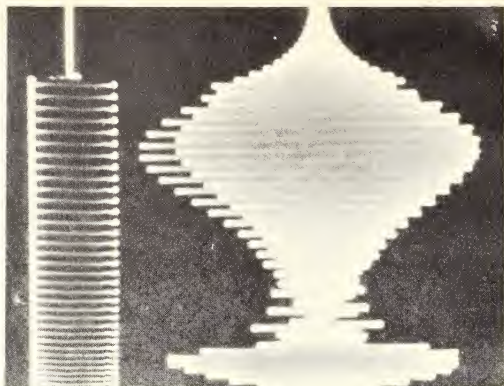
Blocking the nostrils artificially leads to some respiratory stress, but the animals can still fly vigorously. Then the pulses, which are normally of very high frequency perhaps, become clearly audible as the fundamental appears and the spectrograph shows the full harmonic series emitted orally. Occasionally specimens of Glossophaga soricina showed this in the wild, although the reason was not clear.



(c) Chilonycteris rubiginosa (12). Constant frequency followed by terminal sweep.



(d) Balantiopteryx plicata (11). Largely 2nd harmonic with a slight frequency sweep.



(e) Glossophaga soricina (12). Pronounced double peak consisting of fundamental followed by 2nd harmonic.

The rich harmonic structure and the fixed formant frequency make these animals good candidates for testing the effects of light gases. In Artibeus jamaicensis a distinct shifting of the formant structure was found when the animal was made to breathe a small, uncontrolled amount of hydrogen. Although in man this produces an apparently continuous shift in voice pitch, it is the formants that change over a mixture of relatively closely spaced harmonics; the glottis is apparently little affected by the change in loading. The crude experiment on Artibeus similarly showed no change in the glottal harmonic series but gave an upward shift of resonance so that pulses which were previously two-peaked (2nd harmonic then 3rd) gave way to a single peak of the 3rd harmonic halfway through the pulse.

(4) Emballonurid type. Here constant frequency pulses are emitted orally with several harmonics of which the second is often the most pronounced, with the third harmonic and the fundamental at lower levels. This low-Q system gives a complex waveform especially if the frequency falls slightly as in Taphozous. Saccopteryx produces alternate pulses at two different frequencies, perhaps on inhalation and exhalation, which give different phase patterns. A similar effect in Rhynchiscus has been interpreted as a variation in harmonic structure since a fixed phase relation was assumed (5). This now seems unlikely and for Saccopteryx is not supported by spectrographic analysis.

(5) Rhinolophid type. The Rhinolophidae and some Hipposideridae emit long pulses of very constant frequency with sometimes a slight upward sweep at the start and usually a downward sweep at the end. Novick (9)

first noticed that in some species the energy is concentrated in the 2nd harmonic. This is confirmed for four other species of Rhinolophus, including R.ferrumequinum, and for Hipposideros caffer. Despite the apparently sinusoidal waveform, weaker components can be detected at $f/2$ and $3f/2$ with a tuned heterodyne detector.

The pulses are invariably emitted nasally and a nostril spacing of $\frac{\lambda}{2}$ for the principal component (the 2nd harmonic) seems to be the rule. Occluding the nostrils produces extreme respiratory distress and cessation of pulsing, but sick individuals of Rhinolophus ferrumequinum often show a pronounced increase in the proportions of fundamental and 3rd harmonic. Possibly the sharp harmonic selection is associated with the bursa pharyngealis which can become blocked by mucus, but this is just a guess.

The terminal sweep is interesting because its amplitude may fall rapidly from that of the constant frequency, or just as often rise to a pronounced peak before decaying to zero. Pulses of each type may be mixed together within the same pulse train. These patterns are interpreted in the same way as Saccopteryx pulses by supposing that the frequency varies slightly from pulse to pulse. This is certainly supported by heterodyne detectors which effectively magnify the variations and show that quite marked changes occur. If the constant frequency lies above the resonant frequency, the sweep will pass through the peak of its response curve, but if it lies just below, the amplitude will decay rapidly when the sweep occurs.

No experiments with light gases have yet been performed on these bats. It should be possible, by using the right oxy-helium mixture, to

replace the 2nd harmonic by the 3rd. Thus the signal of 85 kHz of Rhinolophus ferrumequinum should decay and be replaced by one of 127 kHz - no intermediate frequencies should be produced. So far no naturally occurring pure 3rd harmonic has been found - even Hipposideros caffer produces 150 kHz above a fundamental of 75 kHz.

These interpretations of the theory as applied to various types of pulse can be examined and quantitatively assessed by means of an electrical analogue model which reconstructs the waveforms obtained under the conditions postulated for each case. This model is a development of the one mentioned earlier, and is constructed as follows.

The core of the instrument is a free-running multivibrator oscillator which represents the laryngeal generator. A saw-tooth generator has been used, but a square-wave generator is better because the mark/space ratio can be varied between 1 and 5 in order to change the harmonic spectrum produced. The frequency of the oscillator is controlled by a voltage waveform similar to that of Fig. 1. This is produced quite simply from the square-wave output of a flip-flop with controlled upper and lower voltage levels. This is then integrated with different rise and fall time-constants controlled by two diodes. The controls provided are therefore 'Upper Frequency', 'Upper Frequency Duration', 'Sweep Time Constant' and 'Lower Frequency'. Another flip-flop starts and stops the multivibrator to give 'Pulse Duration', and both flip-flops are simultaneously triggered by a master pulse generator which determines 'Pulse Repetition Rate'. By adjusting these controls any pattern of Fig. 2 or a number of intermediate patterns can be generated with appropriate time relations.

The output of the multivibrator is then filtered by a simple tuned circuit with variable 'Q' and 'Resonant (Formant) Frequency', which represents the vocal tracts. The pulse waveform can be displayed either before or after filtering and can be translated into sound by an ionophone transducer. It can then be examined by a heterodyne detector or by the tape recording system for time expansion and audible replay or Sonagraph analysis. In other words, it can be treated in every way as a real but controlled bat pulse. The uses of the generator are therefore much wider than the computation of waveforms.

With careful manipulation, either empirically or with the help of data from sound analyses, it is possible to derive a close resemblance to any given pulse recorded from a bat. This is despite the fact that no arrangements are included for shaping the unfiltered pulse - the oscillator is always gated by a square wave. Also no attempt is made to produce asymmetrical filter responses to match those of the real cavities, since these properties are not yet known.

The one variable which is often difficult to predict from either waveform or spectrographic analysis is the Q of the resonant system. Use of the model shows that a range of values from 1 to 10 is quite sufficient, and higher values give ringing effects which have not been observed in bat pulses. A high Q filter closely coupled to the laryngeal generator would be expected to produce some distortion of the sweep by frequency 'pulling' and this also is not found. The waveforms of 'sharply tuned bats' are often reproduced with Q values of 5 or so, and mark/space ratios close to 1. The theory does not make any undue technical demands upon anatomy.

All the problematical features listed at the beginning of this paper can be reproduced in a controlled, predictable and therefore explicable manner. Even the pulses of Phyllostomatids with their nostrils plugged, or those of Artibeus in hydrogen gas can be reproduced by changing the appropriate control settings. This does not of course prove that real bat pulses are derived in the same way, but the close resemblance to some very varied and complex waveforms does lend some credence to the idea. Any participant in the Symposium who may doubt this is invited to handle the generator by himself.

Acknowledgements

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ABSTRACT

Oscillographic displays of the orientation signals of bats show wide variation, from a 'sine-wave' to a complex waveform. A simple electrical model and oscillographic/spectrographic analyses of the pulses recorded from over 60 species of 13 families show that all wave-forms can be derived from a pulsed glottal waveform by vocal-tract resonance. This mechanism resembles that of human vowel production but involves only one formant, relatively low in the harmonic series. Further influences may be introduced by facial appendages, atmospheric velocity-dispersion and the intrusion of echoes when recording. The combined theory adequately explains the time-course of harmonic components, their complicated phase-shifts, different envelope shapes including 'hour glass' and 'terminal peak' patterns and two distinct amplitude modulation effects. It also produces the surprising results that drastic changes between adjacent pulses are more apparent than real, that some high-frequency bats emit 'pure' harmonics and that others are easily rendered audible. Further work involves measuring the predicted properties of passive components in the system, elucidating the newly defined laryngeal function and examining the implications for echo-information theory.

Bats

Ultrasound

Waveform analysis

Harmonic analysis

Acoustic recording

Phonetic theory

Acoustic resonance

Analogue model

DISCUSSION

by

E. J. RISNESS

From an engineer's viewpoint, Dr. Pye appears to have produced a very satisfactory explanation of the observed features of the bat's transmitted waveforms. The statement that the wide variety of bat's waveforms can all be derived by selecting from a limited number of tone pulses, and of rising and falling FM pulses, illustrated in fig. 1, is of particular interest. Is this merely a neat way of classifying these waveforms, or is it suggested that the bat is inherently capable of producing the whole sequence, but only selects part of it to transmit?

The degree to which Dr. Pye has checked that his observations are not artifacts of the situation or measuring equipment, but are genuine variations of the bat's note, is very creditable. Some small points of detail could perhaps be mentioned. A large part of the phase shift in amplifiers is proportional to frequency and hence is equivalent to a time delay which does not distort the waveform. Also in table 2 it is not clear whether the figures quoted refer to group or to wave velocities, which would affect the significance of the table.

It is of interest to speculate on the likely value to the bat of the amplitude and phase variations produced by the modulations described. A simple engineering approach to the problem of signal design for active sonars would suggest that the band-

width of the signal is of prime importance in its performance against a reverberation background and its range resolution. Similarly the duration of the signal affects its performance against a noise background and also its doppler resolution. Amplitude variations are of little consequence (unless one is peak power limited e.g. by cavitation in the underwater case, in which case it is better to transmit at constant amplitude). Phase variation also matters little - it is the relative phase between transmitted and received signal that counts. However, the detailed shape and spectrum of the signal may be important in the presence of interfering signals, e.g. other bats. Has Dr. Pye any evidence that the transmitted waveforms of individual bats are sufficiently different for this to be a significant possibility?

DISCRIMINATION OF THIN WIRES BY FLYING HORSESHOE BATS (RHINOLOPHIDAE)

by
H.-U. SCHNITZLER

The orientation sounds of horseshoe bats were studied by Möhres in 1953. He found that horseshoe bats employ relatively long pulses of constant frequency at a repetition rate of 5 - 6 pulses/sec. The apparatus that Möhres used did not allow a complete analysis of orientation sounds. With an improved recording technique it was possible to record the orientation sounds of flying horseshoe bats. My interest has been focussed on the problem of changes in sound character in different orientation situations, for instance in obstacle avoidance during flight.

Methods

Two species of horseshoe bats were studied, Rhinolophus ferrum-equinum and Rhinolophus euryale. The bats were kept in a room 7.5 metres long, 3.3 metres wide and 2.1 metres high (Fig.1). The room was divided by means of a curtain into a feeding room and a flying room where the bats had their roosts and could fly freely. During the experiments the bats flew from the starting place straight to the landing bar through a 90 cm square gap in the curtain. At the landing bar they were given half a mealworm and then returned to the starting place. A movable frame with vertical wires could be mounted within the gap in the curtain.

This paper gives a provisional summary of some experiments conducted in connection with my thesis which is not as yet completed.

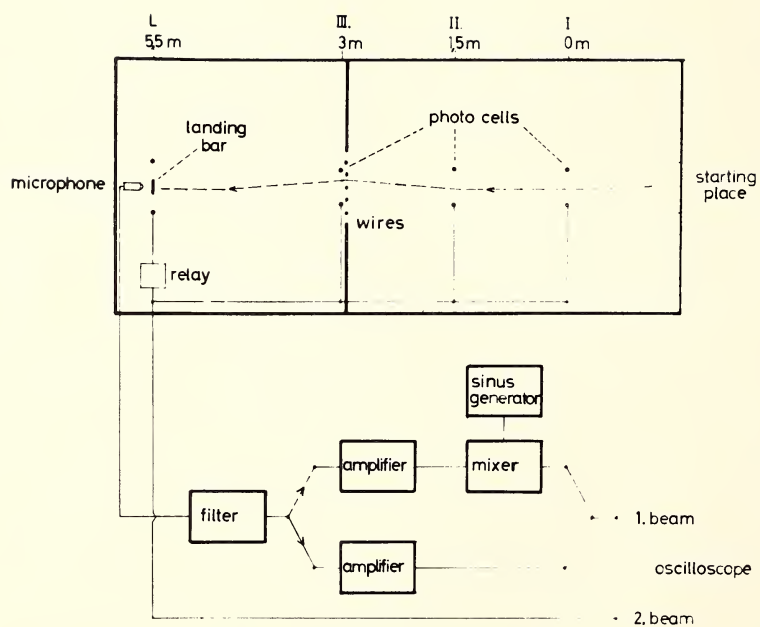


Fig. 1: Diagram of the room used for experiments.

orientation pulse of a resting bat

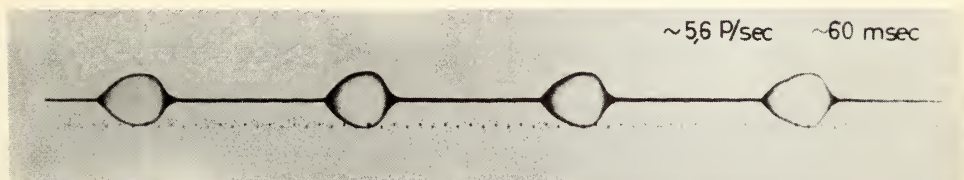


mixed with the proper frequency of 83 Kc



Fig. 2: Orientation pulse of a bat at rest.

orientation pulses of a resting bat



after clicking

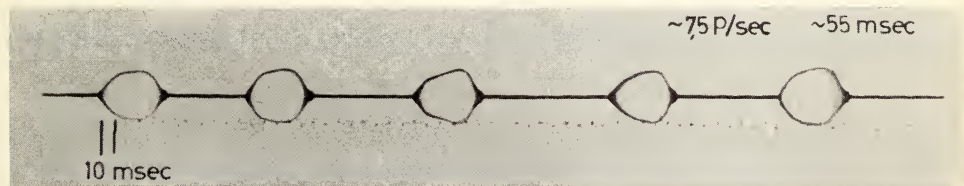


Fig. 3: Orientation pulses of a bat at rest.

The flight route was divided into 4 parts by light barriers with photo cells. The orientation pulses of the bats in flight were detected by a microphone mounted behind the landing bar. They were either recorded directly on a two beam oscilloscope after passing a filter and an amplifier, or were heterodyned with a sinus frequency and then fed into the oscilloscope. The impulses of the photo cells I - III were recorded on the second beam. The photo cell at the landing bar ended this recording by triggering a relay.

Orientation sounds of a bat at rest

Fig. 2 shows the orientation pulse of a bat at rest recorded with high velocity film. The pulse duration was 54 msec. Below, a similar pulse is shown, heterodyned with a sinus frequency corresponding to the bat's own pulse frequency, and the beat frequency is recorded. Sinus and pulse frequency are fully compensated in the long initial part. Accordingly, this initial part has a constant frequency as high as the sinus frequency of 83 kHz. In the terminal part the beat frequency drops by at least 20 kHz. Therefore, this part is frequency-modulated. I found this division into a long initial part of nearly constant frequency, and a short terminal part which is frequency-modulated by at least 20 kHz in all orientation sounds.

The frequency of 83 kHz is a very intensive 1st harmonic of a faint basic frequency of 41.5 kHz.

Fig. 3 shows orientation pulses of a bat at rest. The mean duration is 60 msec at a repetition rate of 5.6 pulses/sec. When a clicking noise occurs the pulses are shortened to 55 msec and

no obstacle

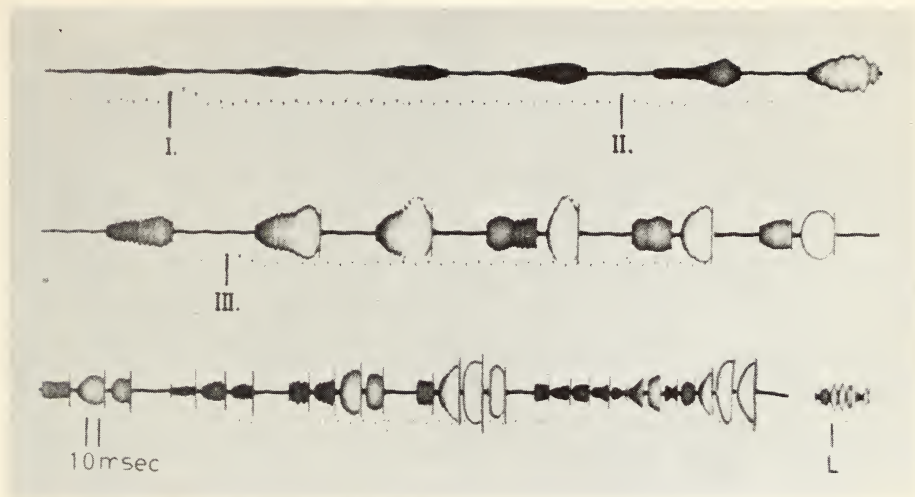
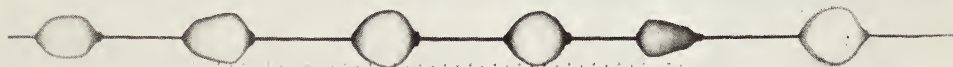


Fig. 4: Recording of the orientation sounds during flight from the starting place to the landing bar.

orientation pulses of a resting bat



- of a landing bat



Fig. 5: Comparison between the orientation pulses of a resting and a landing bat.

the pulse repetition rate rises to 7.5 pulses/sec.

Orientation pulses of a bat flying in an obstacle-free room

Fig. 4 demonstrates the orientation sounds accompanying an obstacle-free flight from the starting place to the landing bar. In free flight a bat initially emits long pulses followed by several groups of 2, 3, and 4 pulses and a final buzz; when approaching the landing bar, of 12 - 20 pulses. All groups, including the groups with one long pulse, have almost the same duration of 100 - 110 msec except the final buzz which is of longer duration. The repetition rate of the groups (9-10 groups/sec) seems to be correlated to the respiratory cycle.

Such a recording only allows one to plot the sound characteristics as pulse repetition rate and pulse duration against a time base. It is of greater interest to use the distance flown as a basis for the diagrams. Therefore, I heterodyned the orientation sounds of the flying bats with a sinus frequency corresponding to the frequency of the bat's own pulses. When the sounds of bats at rest are recorded the sinus frequency and the initial constant frequency of the orientation pulses are compensated. When the bats are in flight the Doppler effect produces a beat frequency which is an exact measure of the flight velocity. This beat frequency was recorded. In this way it was possible to calculate the flight velocity for each orientation pulse and thus to plot a flight velocity/time graph (Fig. 6 a). The area below the curve indicates exactly the distance flown. The distance flown, therefore, during each orientation pulse could be calculated by measuring the corresponding area below the curve. The

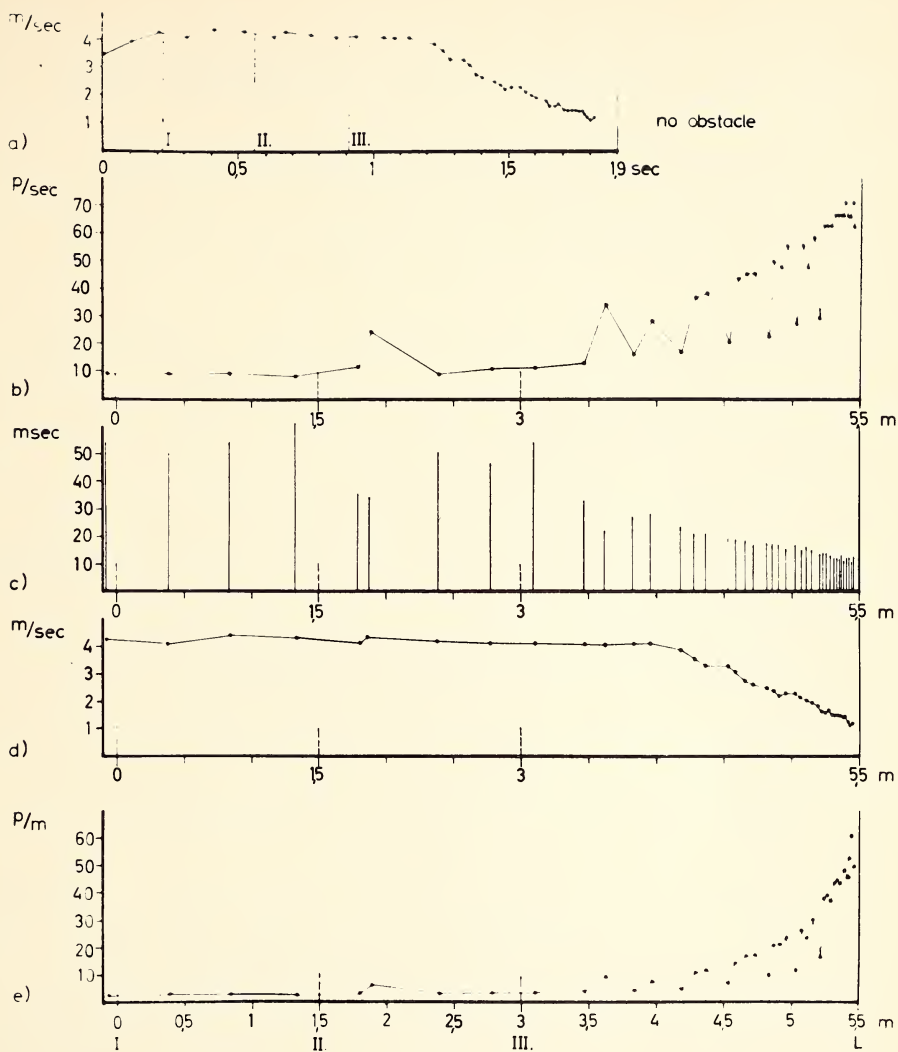


Fig. 6: Sound characteristics of a flight in an obstacle-free room.

- a) Flight velocity - time graph
- b) Pulse repetition rate graph
- c) Pulse duration graph
- d) Flight velocity graph
- e) Pulse density graph

marks of the photo cells made it possible to check this calculation.

Fig. 6 b demonstrates the pulse repetition rate plotted against the flight route. The repetition rate increases about 10 pulses/sec during free flight to 72 pulses/sec in the final buzz.

The pulse duration decreases from an average of 50 msec in free flight to a minimum of 10 msec in the final buzz (Fig. 6c).

The flight velocity remains fairly constant in free flight, and drops when landing (Fig. 6 d).

The pulse repetition rate is to be considered independently of the flight velocity, and therefore it is not a suitable measure for judging the situation of orientation in a flying bat, for a bat with a constant pulse repetition rate emits twice the number of pulses in covering the same distance by reducing its flight velocity by half. For this reason I have used a new term, the "pulse density", which is defined as the quotient of pulse repetition rate and flight velocity. Its unit of measurement is pulses/m.

Fig. 6 e shows that the pulse density rises from 2 - 3 pulses/m in free flight to a maximum of 61 pulses/m in the final buzz.

Comparing the lowest pulse repetition rate with the highest resulted in the ratio of 1 : 6. With corresponding pulse densities the result is a ratio of 1 : 30. In other words, when landing the bats emit 30 times more pulses than during a free flight of the same distance.

If the intensity of the initial part with the constant

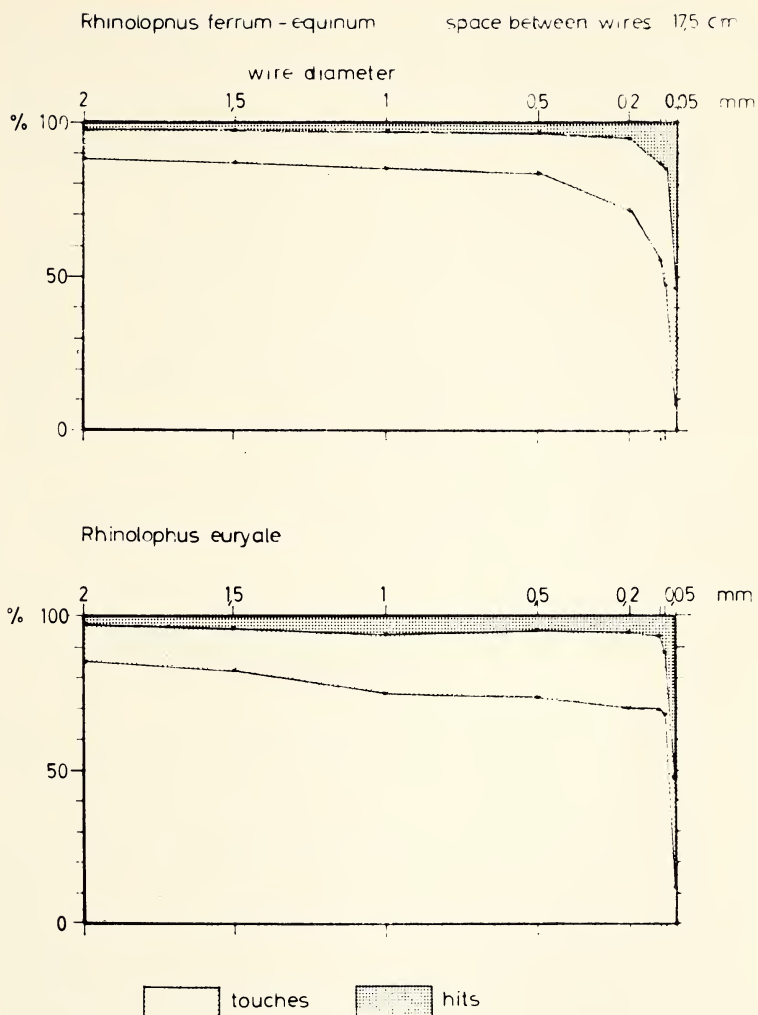


Fig. 7: Obstacle avoidance of *Rh. ferrum-equinum* and *Rh. euryale* flying through a row of vertical wires spaced 17.5 cm apart, but differing in diameter.

frequency and the terminal frequency-modulated part of the orientation pulses are compared, the intensity of the frequency-modulated part is increased in the pulses of landing bats (Fig. 5).

Obstacle of vertical wires with constant space between wires and varying wire diameter

Fig. 7 represents a graph of the percentages of hits, touches and misses which resulted from the bats flying through a movable obstacle of vertical wires of variable diameter and with a constant distance of 17.5 cm between them. This experiment was made with two Rhinolophus ferrum-equinum with a wing-span of 36 cm, and two Rhinolophus euryale with a wing-span of 30 cm. When the diameters of the wires varied between 2 and 0.08 mm, the total of misses was distinctly higher than the optimal chance rate of about 50 %. At 0.05 mm the bats were no longer able to avoid the thin wires. Comparing the number of touches and hits a ratio of 1 : 3 emerges for wires up to 0.08 mm in diameter. This ratio is probably due to inaccurate flight correction. With a wire diameter of 0.05 mm the ratio is 1 : 1. This confirms the finding that the bats are not able to avoid these fine wires.

A study of orientation sounds with different wire diameters produced similar results when the diameters varied between 2 and 0.5 mm. A typical sound sequence at a wire with a diameter of 1.5 mm is shown in Fig. 8. Before passing the obstacle the bat emits a long buzz of 15 - 20 pulses at a pulse duration rate of 10 msec. In Fig. 10 the pulse repetition rate increases to a maximum of 77 pulses/sec, while the pulse duration drops to 10 msec. Furthermore, one notices a considerable decrease in flight

1,5 mm wire - 17,5 space between wires

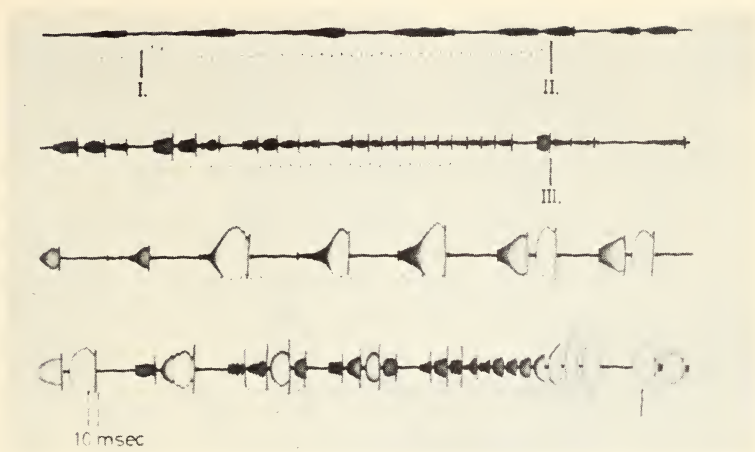


Fig. 8: Recording of the orientation sounds of a flight through an obstacle; wire diameter 1.5 mm, space between wires 17.5 cm.

0,1mm wire - 17,5 cm space between wires

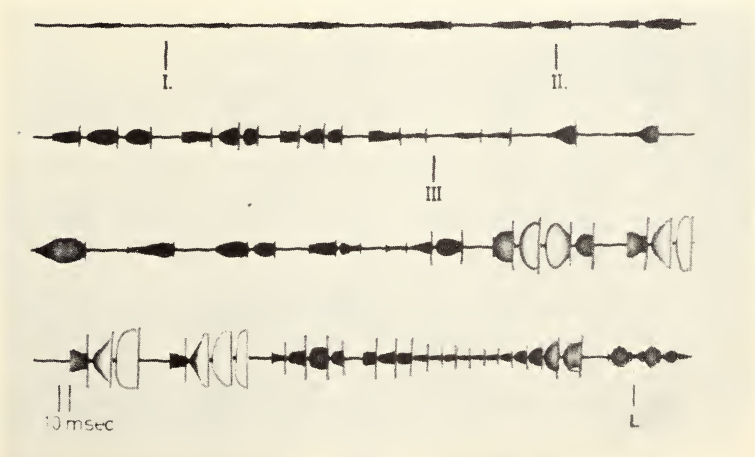


Fig. 9: Recording of the orientation sounds of a flight through an obstacle; wire diameter 0.1 mm, space between wires 17.5 cm.

velocity while the pulse density increases to a maximum of 67 pulses/m.

Using diameters from 0.2 to 0.08 mm another sound sequence appears which is represented in Fig. 9. There is no final buzz before passing the obstacle, and the highest number of pulses per group is 3. The pulse repetition rate increases to only 45 pulses/sec (Fig. 11), the pulse duration drops to a minimum of 18 msec, and the pulse density only rises to 20 pulses/m instead of 60 to 70 pulses/m as in the case of diameters from 2 - 0.5 mm.

At diameter 0.05 mm the bats emitted 1 - 2 groups with 2 or 3 pulses. It is not certain whether the bats actually detect the wires. It is also possible that the small increase in the repetition rate is caused by training on the position of the obstacle. Further experiments will be made in order to solve this problem.

Discussion

According to my results the long pulses are emitted at rest, on starting, and during free flight. On approaching an obstacle or while landing the pulse repetition rate and the pulse density rise, and the pulses are shortened. The bats probably try to gather more information about their environment by measuring distances. This could be a reason why the intensity of the frequency-modulated terminal part is much higher in the short pulses. Such short and intensive frequency-modulated pulses are highly suitable for the measuring of distances.

When the bats rest or fly freely, however, they emit long pulses of constant frequency with a frequency-modulated part of low intensity. It is possible to interpret the meaning of

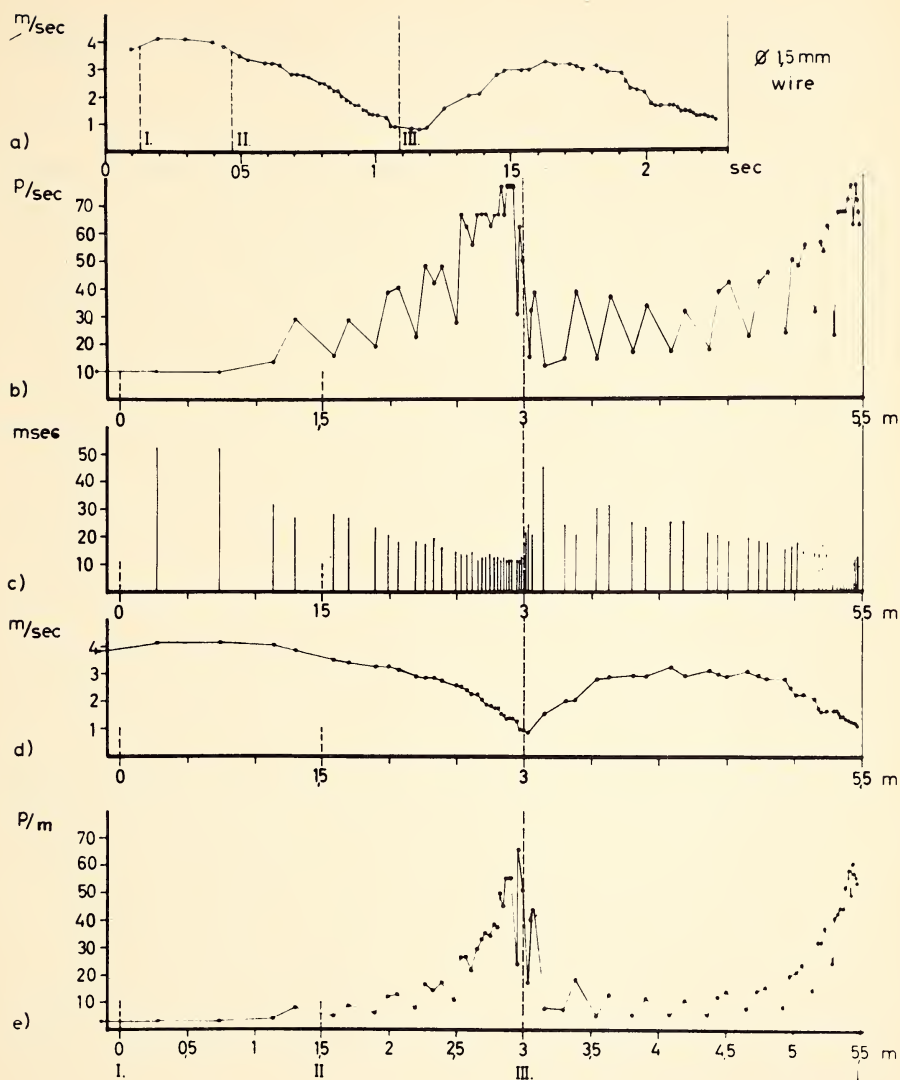


Fig. 10: Sound characteristics of a flight through an obstacle; wire diameter 1.5 mm, space between wires 17.5 cm.

these long pulses in different ways, e.g. Möhres 1953. Another hypothesis follows:

The echoes of the orientation pulses of flying bats show a Doppler frequency shift according to flight velocity. All echoes reflected by motionless objects show this modification. A moving object, e.g. an insect, causes a different Doppler shift. By means of this different frequency any echo from a moving object will immediately attract the bats' attention, and they recognize a moving object. From the sweep of the Doppler shift the bat is even able to detect whether the object is moving away from or towards it. Prolonged pulses render it more probable that all movements are recognized, and the bats therefore, emit long pulses. Once the moving object has been detected the bat emits a buzz with a high pulse repetition rate and short pulses before making its catch. The long orientation pulses of resting bats may serve as an alarm system, since any moving object can be detected by means of the Doppler effect.

These experiments show that rhinolophid bats like all other families of bats, so far studied, increase the pulse repetition rate and pulse density when approaching an obstacle or before landing. It is probable the extremely long pulses emitted by resting and free-flying horseshoe bats are used for the detection of moving objects by means of the Doppler effect. This does not exclude the fact that the prolongation can have a functional importance in other respects.

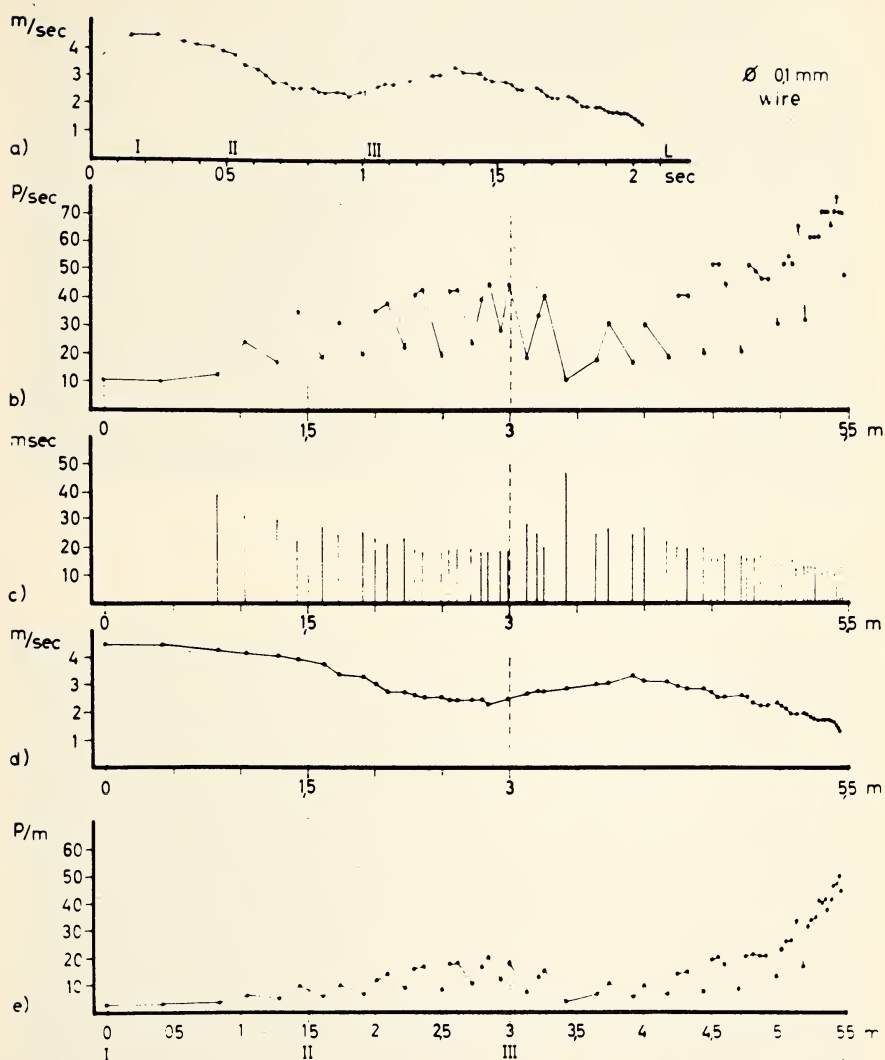


Fig. 11: Sound characteristics of a flight through an obstacle; wire diameter 0.1 mm, space between wires 17.5 cm.



Fig. 12: *Rhinolophus ferrum-equinum* passing an obstacle; wire diameter 2 mm, space between wires 15 cm.



Fig. 13: *Rhinolophus euryale* passing an obstacle; wire diameter 2 mm, space between wires 15 cm.

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Abstract

Rhinolophus ferrum-equinum emits orientation pulses consisting of a long initial part of constant frequency, (83 kHz) and a short frequency-modulated terminal part. While resting or flying freely the bats emit pulses lasting 60 - 50 msec at a pulse repetition rate of 6 - 10 pulses/sec. When landing or passing an obstacle of vertical wires with a diameter of 2-0.5 mm the pulse duration shortens to a minimum of 10 msec, and the pulse repetition rate increases to 70-80 pulses/sec. The pulses are emitted in groups, the repetition rate of which seems to correspond to the respiratory cycle. At wire diameters below 0.08 mm the bats are no longer able to avoid the wires. When the bats land or pass an obstacle the intensity of the frequency-modulated terminal part increases. This part is probably used for the measuring of distances. The long pulses of resting and free-flying bats are interpreted as a special adaptation for detecting moving objects by means of the Doppler effect.

PSYCHOACOUSTICS OF OBSTACLE
DETECTION USING AMBIENT
OR SELF-GENERATED NOISE

by
J. P. WILSON

Introduction

As many factors are involved in the auditory detection of obstacles, it is advisable to place the particular aspect to be considered in context. The simplest type of obstacle is one which emits sound. In this case it is possible to localize it in space relative to the observer in terms of its polar co-ordinates. The azimuth can be evaluated from the interaural intensity difference and, to a lesser extent, the interaural time difference. For broadband sounds extending to high frequencies the complex polar sensitivity diagram of the pinna enables sources of sounds to be localized roughly, both in azimuth and elevation, and possibly to some extent, even in distance. Small movements on the part of the observer give rise to systematic changes in each of the above parameters leading to an enhancement of accuracy, to the resolution of certain ambiguities, and to the judgement of distance from the rate of change of amplitude with distance. In addition to this latter cue the ratio of direct to reverberant sound can give information about distance.

Turning now to silent obstacles we are faced with certain difficulties. It is necessary for the obstacle to reflect enough sound to be heard in the presence of the sound source itself.

This involves both physical and psychoacoustic factors. The physical factors are (a) that the obstacle should be large enough compared with the wavelength of sound to reflect rather than diffract or scatter the sound and (b) that the obstacle, sound source, and observer should be so positioned that the specularly reflected sound should reach the ears of the observer i.e. that the acoustic image of the source should be "visible" in the reflecting surface of the obstacle. It is obvious that a good many natural situations cannot satisfy these conditions. The psychoacoustic factors are involved with the ability of the auditory system to detect the reflected sound in the presence of the direct sound. This can be achieved in two complementary ways (a) by the spatial resolution of source and acoustic image so that each can be heard separately at its appropriate position in space and (b) by the analysis of the combined signal at the ear enabling primarily the path difference to be determined and secondarily something about the nature of the obstacle from the bandwidth of the frequency spectrum changes introduced. These two psychoacoustic factors (a) and (b) are really the crux of the problem and it is unlikely that in any natural situation one will be present without the other. The efficient functioning of (a) requires two ears including pinnae and frequency components extending towards the upper limit of hearing whereas (b) can operate quite adequately through a single microphone and headphone and need not include the highest frequencies. Indeed this cue can be perceived more readily under these conditions

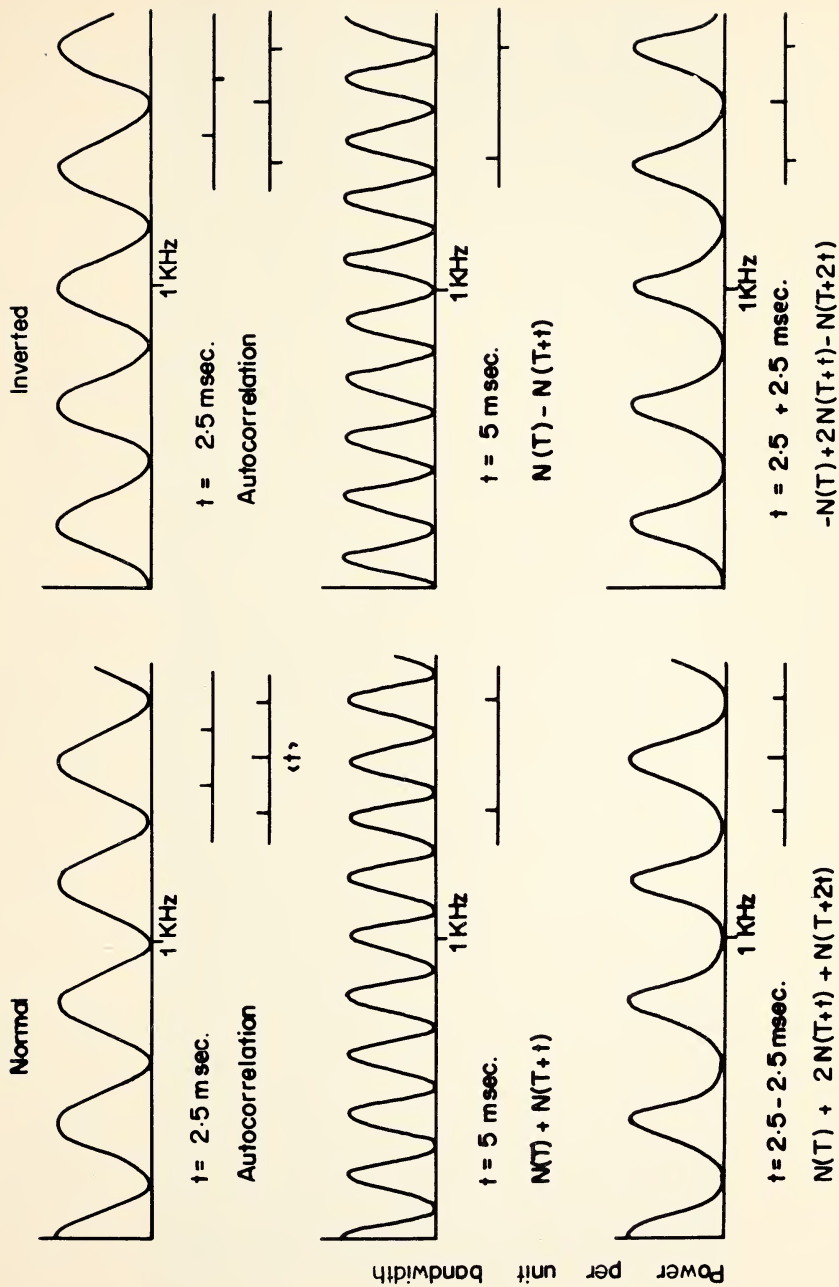


Fig. 1

than naturally although it is unlikely that there is any significant difference in its magnitude over the range of frequencies for which it is most effective. It is this monaural cue, the reflection tone, with which this paper is chiefly concerned.

Theory of the Reflection Tone

When a reflected sound wave is added to the direct sound wave arriving at the ear physical interference takes place so that some frequencies are reinforced and others cancelled. The frequency spectrum is modified so that the pressure P for any frequency component f becomes

$$P = P_0 (1 + a^2 + 2a \cos 2\pi ft)$$

where (a) is the relative amplitude of the reflected wave and t , the time delay of the reflected sound relative to the direct sound. This means that a "white" noise would become modified and would no longer contain equal energy for each unit frequency bandwidth but would have a series of peaks at frequencies

$$\frac{c}{s}, \frac{2c}{s}, \frac{3c}{s}, \frac{4c}{s} \dots\dots\dots$$

and dips at frequencies

$$\frac{c}{2s}, \frac{3c}{2s}, \frac{5c}{2s}, \frac{7c}{2s} \dots\dots\dots$$

where c , is the velocity of sound and s the path difference (Figure 1). The peaks are widely spaced for small delays or small path differences and closely spaced for long delays and long path differences. Figure 2 shows a Sonogram for delays in

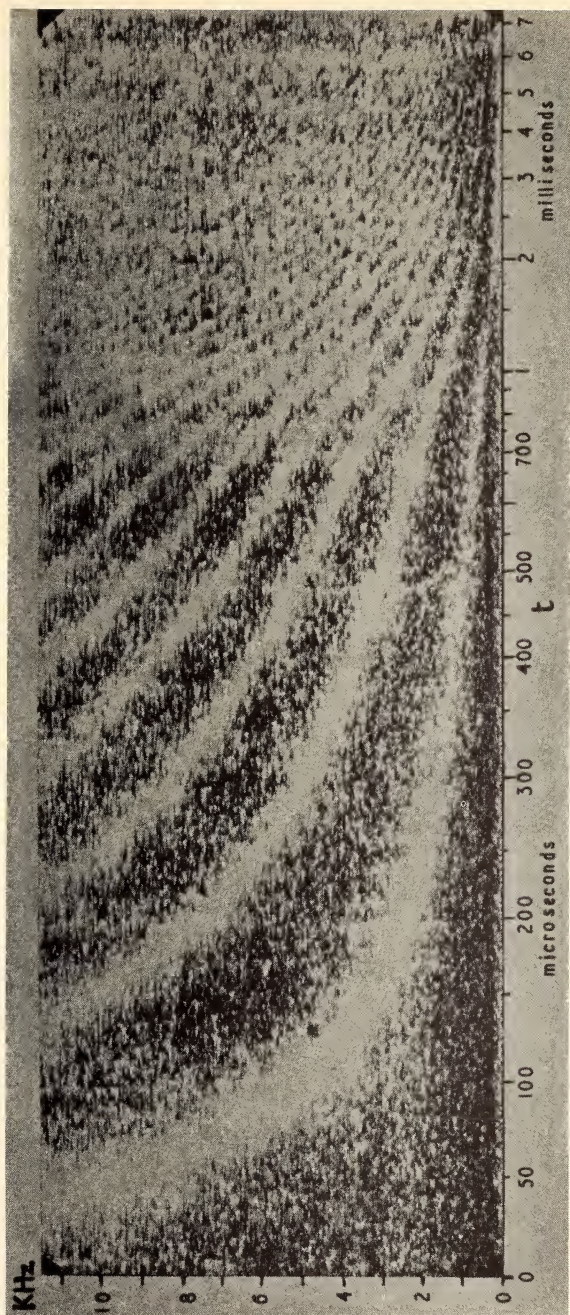


Fig. 2

the range 0-7 milliseconds. This information about path difference or range is of course also available in a time analysis. The auto-correlation function is illustrated also in Figure 1, but a simple additive correlation would also yield this information. This can be demonstrated by superimposing several traces on an oscilloscope each triggering when, for example, the wave passes positively through zero. Thus the presence of these frequency spectrum modifications does not necessarily imply that the ear analyses the signal in this way. What observers report hearing is a tone whose pitch gets higher as the path difference decreases (1, 8). The pitch of this tone corresponds to that of the frequency of the first peak in the spectrum or $\frac{1}{t}$. A theoretical graph relating pitch to path difference is given in Figure 3.

Geometrical factors

The effectiveness of this pitch cue to distance will depend on the geometrical arrangement of source, reflector, and observer. In the general case the path difference will be given by

$$s = \sqrt{x^2 + z^2 + (b + y)^2} - \sqrt{x^2 + z^2 + (b - y)^2}$$

where b is the perpendicular distance of the source from the reflecting surface, y is the perpendicular distance of the observer from the surface, and x and z the longitudinal and vertical differences in coordinates between source and observer (Figure 4). This expression can be simplified in a number of ways, e.g.

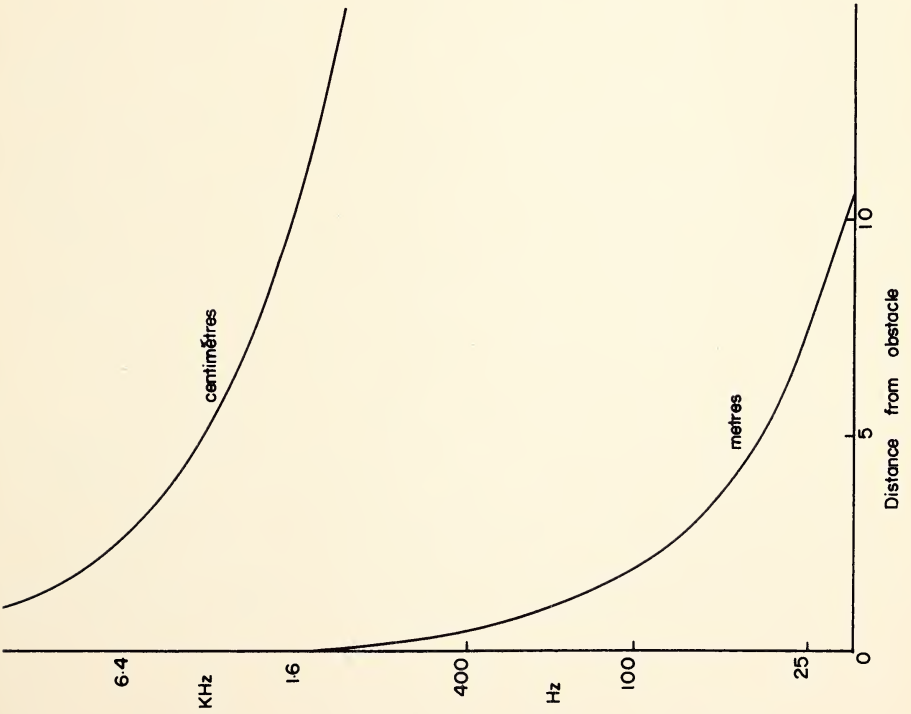


Fig. 3

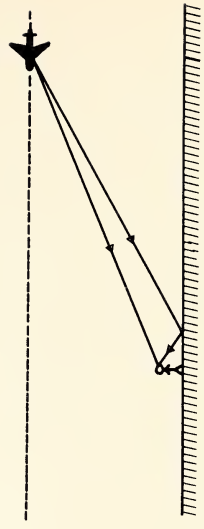
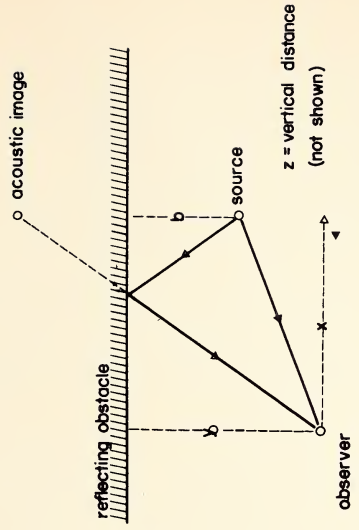


Fig. 4

- (i) if $x=0$, $z=0$ and $b > y$, $s=2y$
- (ii) if $x=0$, $z=0$ and $b=y$, i.e. if the observer carries the source of sound, $s=2y$
- (iii) if $x=0$, $z=0$ and $b < y$, $s=2b$ i.e. the pitch would

then depend on the position of the source but not the observer. This particular situation would not necessarily be of any significance in practice because the source of sound itself would have to be negotiated before the reflecting surface could be considered as an obstacle.

Situations in which the source is at a considerable distance, i.e. $b \gg y$, are desirable so that the ratio of the path lengths can be near unity. The relative amplitudes will then also be near unity allowing high spectrum modulation depths to occur.

The ideal arrangement would have the further constraint of observer and source lying in a line normal to the surface giving a path difference just twice the distance of the ears from the reflector and independent of small changes of angle of the source. In general the path difference for a distant source at an angle θ from the normal will be $s = 2p \cos \theta$ where p is the perpendicular distance of the observer from the surface. An everyday condition in which this change of pitch with change of source angle is readily perceivable occurs when an aeroplane passes overhead. In this case the effect depends on a ground reflected wave and the perpendicular distance, represented by the height of the ears from the ground, is constant but, θ , the angle between the aeroplane and the vertical is varying. The pitch therefore starts at a high value falls to a minimum when the

aeroplane is overhead and rises to a high value again. (This should not be confused with the Doppler effect which depends on the speed of the aeroplane and in which the whole spectrum of sound is shifted upwards on approach and downwards on recession).

The implication of this dependence on source angle for the blind man is that to utilize the information fully he would have to make a correction which would depend on his perceiving both the direction of source and direction of reflection.

In most natural situations and particularly indoors many reflections occur. Some of the distance such as from floor and ceiling remain constant, and are not required by the blind man, but the possibility of confusion with relevant path differences exists. Generally the nearest object, giving the highest pitch, will be the most important so that the auditory system might conceivably be organized to give priority to the highest pitch. An effect which might support this suggestion has been described by Thurlow. When two identical regular trains of pulses are combined so that an alternation of long and short time intervals occurs a pitch corresponding to the shorter but not to the longer time interval can be perceived (10).

A further complication may, however, arise with multiple reflections when the time interval between two successive reflections may be less than that between the direct wave and the first reflection. It is again possible to postulate a system of priorities ordered in time sequence but there is no real evidence

on this point.

Dynamic Factors

Many of the difficulties and ambiguities outlined above can be resolved when dynamic aspects of the situation are included (12). Movement of the observer will cause some path difference to increase and others to decrease and the change of pitch caused by a given amount of movement is itself a measure of the distance to the obstacle in the direction of motion. To digress slightly it has been found that subjects report the pitch as musical in nature for these types of signal, and are able to place them accurately on the scale within a particular octave but are not certain within which octave they occur. There are two points which arise out of this observation: the occurrence of octave errors indicates the possibility of making related errors in distance judgements (i.e. judging $\frac{1}{4}$, $\frac{1}{2}$, $\times 2$, $\times 4$, the true distance) and secondly that musical interval or the logarithm of frequency, $\frac{df}{f}$, should be considered as the basic scale rather than frequency itself.

Returning now to the effects of a small movement of the observer, dx , it follows that as $f = \frac{1}{t} = \frac{c}{s}$, $\therefore \frac{df}{ds} = \frac{c}{s^2}$

$$\text{and } \frac{df/f}{ds} = - \frac{1}{s}.$$

(This type of relationship for motion parallax is quite general and could alternatively represent the change in loudness of a point source of sound or the change in relative size of a retinal image). It can be seen by inverting the expression that

the distance of the obstacle in the direction of motion is directly proportional to the amount of movement, ds , required to produce a given musical interval, $\frac{df}{f}$.

$$s = ds \left(- \frac{1}{df/f} \right).$$

These equations are independent of the angle of the source and are insensitive to octave errors. Furthermore, the difficulties due to the presence of reflecting surfaces such as floor and ceiling, and to successive reflections from adjacent objects would no longer arise because these would remain constant during normal motion.

When an observer is moving quickly he will take longer to stop. These higher speeds, however, will also give rise to greater rates of change of pitch with respect to time or, alternatively, a given rate of change of pitch will be achieved further from the obstacle. As the rate of change is proportional to velocity and inversely proportional to the distance it follows that once a certain critical rate of change has been achieved the observer will have a constant time, T , before collision whatever his velocity, v .

$$\frac{df/f}{ds} = - \frac{1}{s} \quad \text{but} \quad v = \frac{ds}{dt}$$

$$\therefore \quad \frac{df/f}{dt} = - \frac{v}{s} = - \frac{1}{T} \quad \text{or} \quad T = - \frac{1}{\frac{df/f}{dt}}$$

An experiment of Leonard and Wycherley (5) gave stopping

distances proportional to speeds up to about 8 kilometre/hour for a blindfolded subject. The stopping distances they found for this observer were approximately 70cm/metre/sec. i.e. a value of $T=0.7$ secs. (This would give the subject 1.4 seconds to stop with uniform retardation). Substituting $T = 0.7$ in the above expression gives $\frac{df/f}{dt} \approx 1.4$ which is approximately 2 octaves/sec. This critical value for rate of change of pitch lies well within the range encountered in the rise and fall of formant frequencies in normal speech. It is not unreasonable to suppose, therefore, that the ear may be sensitive to such signals. Furthermore, in the case of the cat, cortical neurones have been found which respond only to certain of changing pitch and not at all to steady tones (11). Although the absolute frequencies are much higher in the case of the cat the rates of change are comparable (1-5 octaves/sec).

Types of Signal

The type of signal considered so far has been continuous 'white' noise. There are, however, many kinds of suitable signal both continuous and transient. Single short impulses or clicks have been used extensively (6, 9, 10): a single click has a continuous spectrum like white noise and the introduction of a second click by reflection, for example, introduces identical modifications to the spectrum. The difference between a click and white noise lies in the relationship between the phases of the component frequencies and this is not available in a frequency or auto-correlation analysis. It may be more infor-

mative to consider figure 1 not as a spectrum but as a filter or a weighting function. In order to make the information in this filter function available to the ear it is necessary that the signal used should provide a test discriminating between the possible alternative filter functions. A line spectrum containing several lines per peak in the function should be satisfactory in this respect. Similarly as the shape and spacing of the peaks is similar throughout the filter a small section containing only a few peaks should be sufficient. It follows that differentiated or integrated noise and various complex transient signals are also satisfactory.

It is, however, possible that further information may be available in this filter function. A small obstacle, for example, will not reflect the lower frequencies effectively so that the modulation depth will be lower at these frequencies. Similarly if the obstacle absorbs certain portions of the spectrum these will lead to correspondingly lower modulation depths. A rather more exotic example would be a dispersive reflecting medium in which different frequencies were reflected from different depths or frequency dependent phase changes introduced. In these cases the spacing between peaks in the filter function would depend on frequency. These examples each offer at least the possibility of some form of obstacle recognition over and above the detection of distance.

The first half of this paper has been a theoretical consideration of the problems involved in the use of the reflection

tone by a blind man. The second half of the paper will describe experiments designed to answer some of the problems raised above and to understand the basis of the perception of pitch in the reflection tone. This study is not yet complete and will be presented in greater detail elsewhere.

Apparatus

The stimulus signal used was electrical noise generated in a stabilizer tube covering the audible spectrum (-3dB at $< 20\text{Hz}$ $> 20\text{KHz}$). This was recorded by two staggered heads on a Brenell tape deck at 38 cm/sec. and played back also by staggered heads. One of these was adjustable along the length of the tape by means of a micrometer screw allowing relative timing between the tracks of the tape of ± 30 milliseconds (or correspondingly greater times at the lower speeds). The frequency response of the tape recorder was within $\pm 3\text{ dB}$ from $40\text{ Hz} - 25\text{ KHz}$. Speed accuracy and constancy were adequate for the experiments described. The signals were presented to the subject via Sharpe HA 10 headphones. Sound pressure levels were set using a B & K 4133 microphone and a flat plate coupler.

(1) Range of time intervals

The lower limit for detecting the reflection tone is rather ill-defined. Below $200\text{ }\mu\text{secs.}$ the tone becomes progressively less musical in nature but changes of sound quality persist right down to $20\text{ }\mu\text{secs.}$ (The reason for this may be appreciated by looking at the Sonogram; Fig. 2). At the other end of the

scale the tone also becomes less musical and tends to sound "periodic". Above 25 millisecs. the signal becomes indistinguishable from a pair of independent noises. It is obvious that as the shortest time interval that sounds different from zero is 20μ secs., corresponding to a path difference of only 7 mm., there is no significant lower limit for the blind man. The upper limit, however, may be of considerable importance and corresponds to a path difference of 10 metres (obstacle distance 5 metres). This is about twice the distance found by Supa, Cotzin and Dallenbach in non-ideal practical situations. (8).

(2) Threshold for a Weak Reflection

This experiment was designed to show up differences between thresholds (a) when the weaker signal comes first or second (b) of normal sum of the signals or differenced sum of the signals (Fig. 1 spectral peaks and dips reversed) (c) sound pressure levels of 30, 60, and 90 dB re $.0002\mu$ bar for the stronger signal and (d) for a range of 10 time delays from 45μ secs to 23 millisecs.

(a) For continuous noise there is no difference in threshold when the weaker signal precedes the stronger one. This is contrary to results obtained when using clicks. Thurlow (9, 10) reported that the weaker signal could be -26dB when it precedes the stronger signal but only -11dB when following the stronger. Gillespie (4) found much smaller differences but these were dependent on the time delay concerned. These differences have been

explained in terms of the difference between backward and forward masking. As the mean intensity level in a continuous noise signal is constant it would appear reasonable that no such difference should exist for noise.

(b) No difference in threshold was found between the normal and inverted (Fig. 1) type of signals. This was not altogether expected because the tone is clearer and less ambiguous in the normal case. It would appear, however, that the threshold is set by the ability of the ear to detect changes in the spectrum envelope or filter function, at a fairly low level in the system. This view is reinforced by finding (d) below in which the lowest thresholds were found for the shortest time intervals where the tone is not well defined.

(c) There was no significant effect of intensity level over the range employed (30, 60, and 90 dB for the stronger signal). This rules out completely the hypothesis of Eastmond and Bassett (1) based on non-linearity of the ear as this does not occur below 40 dB (2). This result may also be considered surprising when it is realized that for the shorter time delays the actual threshold for the weaker signal approached -30 dB relative to the stronger one. This would place it at absolute threshold for the 30 dB signal. In other words if we take a noise signal at absolute threshold and add 30 dB of correlated noise to it we do not impair its detectability (or at least not by more than 3 dB when allowance is made for possible experimental error). With equal signals the reflection tone can be

detected down to about 3 dB above threshold. As ambient noise never approaches such a low level the blind man will never be short of sufficient noise to detect obstacles.

(d) As mentioned above the lowest thresholds occur for the shorter time intervals, 45-180 μ sec, at about -25 to -30 dB depending on the observer; above this they gradually rise until they reach -10 to -20 dB at 23 milliseconds delay. It would appear from this that detection depends on amplitude variations throughout the spectrum rather than the excitation of a specific pitch mechanism. In this respect it might be compared to the intensity difference limen. The lowest threshold obtained, -30dB, would represent an increase of 0.3 dB at the peaks and a decrease of 0.3 dB at the troughs on switching in the weak signal (i.e. a total change of balance in the signal of 0.6 dB).

From a practical point of view it is convenient to take 20 dB as a lower limit as this would then include the majority of observers over the time delay values most important for obstacle detection. As 20 dB represents a path length ratio of 10:1 or an energy absorption coefficient of 0.99 (rarely achieved by acoustic tiles even at the most efficient part of their spectrum) it is unlikely that either of these factors above would prove a limitation in most circumstances.

(3) Pitch of the Reflection Tone

For the normal type of signal the pitch matches obtained correspond to the frequency of the first peak in the filter function, i.e. $\frac{1}{t}$, or to octaves of this. There is a tendency,

however, for octaves to be misplaced towards the centre of the range from both extremes.

For the inverted spectrum signal (Fig. 1) the pitch tends to be slightly different from the corresponding normal signal (i.e. the pitch does not correspond with $\frac{1}{t}$). It is necessary in this experiment to use subjects with a good musical ear for pitch.

Several techniques have been used for measuring pitch. t has been adjusted to match a sine and a square wave; t for the inverted signal has been adjusted until the pitch sounds the same as for a normal reflection tone signal; musical interval judgements have been made for the jump in pitch obtained when switching between the normal and inverted signals for a variety of time intervals; one musician brought along his own tuning fork and with the aid of this made interval judgements so placing each signal on the musical scale (with "sharp" or "flat" corrections).

All these techniques lead to similar results.

(a) Below 250μ secs. delay the inverted signal was generally reported higher. In the more important part of the range above 250μ secs. the inverted signal was generally reported lower.

(b) When a particular inverted signal was heard to change oppositely to the general rule in (a) above, the musical interval concerned was similar. This is contrary to what Thurlow (9) reported for clicks.

(c) The magnitude of the interval ranged from about a semitone (1:1.06) at 25 millisecs. up to about 3 semitones (1:1.2) at 1 millisec. Above this the interval probably increases still further but it becomes possible to make several alternative matches for a given signal and the result is not so clear cut.

This variation is contrary to the results of Fourcin (3) who reported a constant interval of $\frac{7}{8}$ (1:1.14) for all time intervals. Nor does it fit the hypothesis and experimental results of Nordmark (personal communication) (6) who maintains that the lower pitch of the inverted signal can be interpreted as an additional constant time delay.

(4) Filter Experiments

(a) The time interval was set to 2.5 millisecs and the signal passed through an Alison 2 AB bandpass filter (30 dB/octave) with a constant bandwidth of 200 Hz centred on a range of frequencies 300, 500, 700, ... 2,500 Hz. Only for the first three settings did the relative pitch of normal and inverted signals appear to be determined by the nominal pass band of the filter. Beyond this the outcome was in agreement with result 3 (a) above. Thus the pitch does not depend on the presence of a certain critical region of the spectrum. It should be stated, of course, that energy outside the nominal pass band of the filter must have been contributing to this result.

(b) Individual high pass and low pass filtering indicated that the presence of the first four spectral peaks is important

only to the timbre or quality of the sound and not to its basic pitch.

(c) A high pass filter was used to determine how many of the lower peaks could be removed before the reflection tone disappeared. This was done by using a nominal 2 KHz derived filter in which all energy below 1.7 KHz was below absolute threshold. The time interval was then increased until the reflection tone could be only just perceived. This value (21 milliseconds) indicates that only peaks above the 32nd were contributing to the tone. The removal of the first 8 peaks appeared to have no detrimental effect on the subjective strength of the tone. It is unlikely that such closely spaced frequency components could be analysed by the cochlea.

(5) Phase Shifting Experiments

It is possible to obtain a continuous sequence between the normal and inverted extremes of the signal by the use of all pass phase filters and multiplication circuitry. For this experiment the band width was limited to 150 KHz - 4 KHz as only over this region were the outputs of the phase filters in quadrature. The result of this operation on the spectrum is that that position of the peaks and troughs is moved continuously upwards or downwards depending on the direction of rotation of the phase vector applied to the other input of the multipliers. This other input was provided by a very low frequency oscillator the frequency of which determines the number of peaks per second passing a given point on the spectrum (The position of the total

band of noise remains unaltered in contradistinction to the effect of a frequency shifter).

The effect of this on the ear is a sort of auditory "barber's pole" impression where pitch rises or falls continuously. The ear would appear to be following the position of individual peaks in the spectrum. The effect could not be heard, however, for signals with a time delay greater than 10 millisecs. This suggests that for signals between 10 and 25 millisecs. the ear cannot resolve the spectral components and must be operating exclusively on temporal analysis.

(6) An Auditory Negative After-Image

If after listening to a reflection tone signal for a little while one of the components is switched out, or the phones are switched to a single independent noise source, a transient tone can be heard which sounds like the inverse of the stimulating tone. Quantitative measurements were made on this after-image in two ways (a) by matching and (b) by compensation.

(a) A 5 sec. stimulation period was followed by a 5 sec. test period of noise alone during which the after-image decayed away. At the end of this period a real signal, the inverse of the stimulating signal, was introduced. This was adjustable both in initial amplitude and in rate of decay. The task of the subject was to adjust these two parameters until this real signal matched exactly the subjective after-image. These parameters were then measured electrically. The values determined by one subject were an initial amplitude or modulation depth of 37 %

(compared to the stimulating modulation depth of 100 %) and an exponential decay time constant of 0.7 secs.

(b) In the compensation or cancellation method the modulation depth of the signal was suddenly reduced at the end of the stimulation period and then decreased exponentially to zero. In this way the negative image can be just cancelled by the decaying positive signal. This, of course, differs from the matching experiment in that actual positive stimulation continues during the test period. This may be reflected in the results which, for the same subject, gave a modulation depth of 44 % and a decay time constant of 1.2 secs.

One advantage of the matching method is that it is very easy to check on the pitch of the after-image. In all cases, and for several subjects, the pitch and timbre of the after-image were identical to those of the negative matching signal.

The above experiments provided similar results for normal and inverted stimulus signals and for 30, 60, and 90 dB S.P.L. The latter finding shows that this type of after-image is more general than the after-images reported by Rosenblith et al (7) and Zwicker (13) which were fairly critically dependent upon stimulus intensity.

Preliminary tests also indicated that the time constant of build up may be similar at about 1 sec.

The after-image does not appear to be dependent on high values of modulation level for its existence. It does not occur for time intervals above 10 millisecs but below this it

shows little variation in time constant throughout the range. Taken together these results indicate a fairly basic function of audition that probably represents adaptation within the frequency analysing area of the cochlea.

It would undoubtedly account for the frequent report that the reflection tone is much more readily perceivable when the time interval is changing (12).

(7) Double Delay Experiment

The tape recorder on which these experiments were performed has 4 tracks so that it is possible to pass a signal twice through the machine. When this is done the output contains three components; a central one, of double amplitude, separated by t from each of the other two components (Fig. 1). The spectrum of such a signal has peaks and troughs in the same position as before but the spectral bands are narrower and better defined. It is possible to obtain normal and inverted spectra as before. The pitches of these signals are identical to those of the corresponding single delay cases although considerably clearer. This similarity of pitch would not be predicted by a theory invoking an additional time delay to explain the lower pitch of the inverted signal.

Conclusions

It is possible to draw a number of definite conclusions from these experiments even though the details of the mechanisms involved in the perception of pitch remain obscure.

1. The pitch is not determined solely by the spacing of the spectral peaks.
2. The pitch is not determined by the position of the fundamental component of the harmonic series of peaks.
3. No particular region of the spectrum is necessary for the phenomenon.
4. There are circumstances in which a reflection tone can be heard when spectral resolution would not appear to be possible.
5. The pitch is not determined by an auto-correlation function.
6. Several factors associated with this phenomenon appear to require the spectral resolution of the signal and in most cases the known resolving power of the cochlea enables at least part of the spectrum to be so resolved.
7. For the shorter time intervals it would appear that frequency analysis alone is responsible.
8. The phenomenon is not due to non-linear distortion in the ear.

Many diverse factors are involved in the auditory detection of obstacles. Within the physical limitations of the stimulus situations man is well adapted to make use of the meagre information that is available.

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ABSTRACT

In the neighbourhood of an obstacle sound reaches the ear of an observer both directly and by reflection from the obstacle. Interference between these signals introduces a series of maxima and minima into the spectrum, the positions of which depend on the path difference. A sound of broad bandwidth takes a pitch which becomes higher as the obstacle is approached. In addition to the pitch itself, it is likely that rates of change of pitch are important parameters in the avoidance of obstacles.

In order to investigate the phenomenon more fully a signal of this nature was generated on a tape recorder and modified in a number of ways. When one of the interfering signals is sign inverted, a pitch is heard which cannot be explained exclusively in terms of frequency or time analysis. A negative after-image of this reflection tone is also described.

Obstacle detection
Pitch
Reflection tone
Acoustic interference
Auditory after-image

ULTRASONIC ORIENTATION IN MEGADERMATID BATS

by
F. P. MÖHRES

Up to the present time we have had scant knowledge of ultrasonic orientation in the Megadermatidae bat family, the so-called false-vampire bats of the Old World tropics. All the information we had was based on the occasional and fragmentary observations and experiments of MÖHRES and KULZER (1957) and NOVICK (1958). In the last few years we have been successful in maintaining in our Institute a healthy and vigorous group of Megaderma lyra from India which we tamed and trained for experiments. This made possible a more complete investigation than had been done before of the sonar system and orientation ability of these bats. The research was carried out in cooperation with G. NEUWEILER.

Earlier studies of ultrasonic orientation in Megadermatid bats had already given promise that further research would be profitable. Members of the Megadermatidae family have conspicuous nose leafs and gigantic ears (Fig. 1). They fly with admirable skill in complete darkness and in surroundings crowded with obstacles. Unlike many other bats, they possess rather large eyes, and optical orientation seems to be more important than in other groups. Their high degree of precision in orientation is very surprising, especially as the orientation signals appear to be extremely weak. The term "whispering" bats coined by GRIFFIN for bats of a subfamily of the family Phyllostomatidae (bats using signals of very low intensity for echolocation) may be applied to Megadermatidae. In comparing the signal intensity of bats of the same size in the two families of Rhinolophidae (horseshoe-bats) and Megadermatidae, it was found that Megadermatid bats use signals having only 1 % of the intensity of those of the Rhinolophus bats.

Megaderma lyra is not an easy experimental animal. It is very shy and extremely sensitive to noise, and much experience and patience is needed to tame and train



Fig. 1

it for experiments. Megaderma lyra is a rather big bat, the fore-arm measuring on an average 65 mm. This species can be easily distinguished from other species of the same family by the special shape of its nose leaf. Like all members of the family, Megaderma lyra has huge ears, the inner basal margins of which are fused together. The tragus is long and bifurcate. Megaderma lyra is a nocturnally active bat which does not go out hunting before complete darkness has fallen. Unlike other bats, it is not predominantly a flying-insect eater, but hunts for sitting or crawling small animals (both insects and vertebrates) nearly as big as itself. While searching for prey its flight is slow and often hovering. On other occasions the flight may be rapid, but it is always elegant and skilful.

Our research was mainly focused on two points:

- 1) the study of orientation sounds as such to determine the parameters of those signals as completely and exactly as possible,
- 2) the study of the performance and efficiency of the sonar system.

For recording and analysis of the orientation signals standard laboratory methods, with some special improvements, were used. To control the efficiency of ultrasonic orientation the animals were trained to pass grids built of transparent nylon wires of varying diameter and arrangement. During part of these passage experiments orientation signals were continuously recorded.

Character of the orientation signals

a) frequency pattern

As NOVICK (1958) has already started, the orientation signals of Megaderma lyra have harmonical structure. They consist of harmonics of only one basic frequency having an average of 19,6 kHz. Two types of signals may be

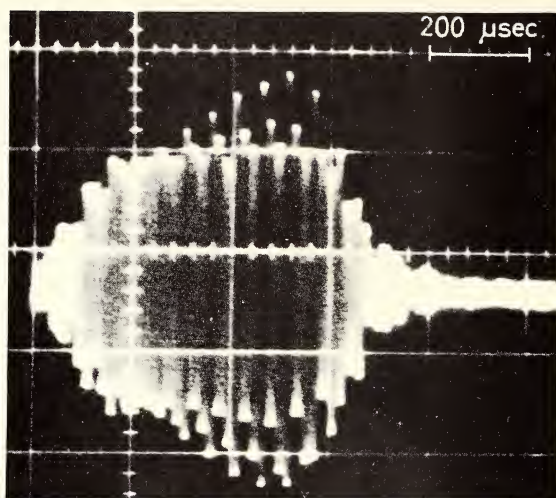


Fig. 2



Fig. 3

distinguished: sounds in which the highest frequency present is the third harmonic, and other sounds, the highest frequency present of which is the fourth harmonic. The frequencies present remain constant throughout the whole pulse, while the intensity may vary, even to the degree that one or the other of the harmonic frequencies is absent in parts of the pulse, principally in the beginning (Fig. 2). The most intense frequencies in the pulses are 58,5 resp. 78,5 kHz, the intensity relation of these two principal frequencies being variable. The basic frequency of 19,6 kHz is not found in the records. It is either extremely weak so that it escapes recording, or it is already lacking in the pulse itself. Sometimes, if only the fourth very intense frequency is present, the pulses begin as pure tones. Later on other harmonics begin to appear. In general, orientation signals of Megaderma lyra show much more variety than NOVICK originally found.

b) pulse duration

Compared with the orientation sounds of other bats the pulses of Megaderma lyra are extremely short (Fig. 3), the shortest pulse recorded lasting no longer than 420 μ sec., and the longest one lasting 1760 μ sec. The pulse duration thus varies for 1300 μ sec. This variation is related to the orientational situation. The longer signals, which are pulses in the lower frequency range, are produced in free and unimpeded flight in open space. Shorter (less than 1000 μ sec.) and higher frequency sounds are produced by non-flying bats exploring the environment, and by flying bats in approaching a goal or obstacle. The number of single waves in a pulse is rather constant and independent of either duration or pitch. The average value is 42 single waves in a pulse. When there is no change in intensity, the signals, whether short or long, high-pitched or low-pitched, have nearly the same energy content.

c) intensity of pulses

It is extremely difficult to satisfactorily measure the intensity of orientation

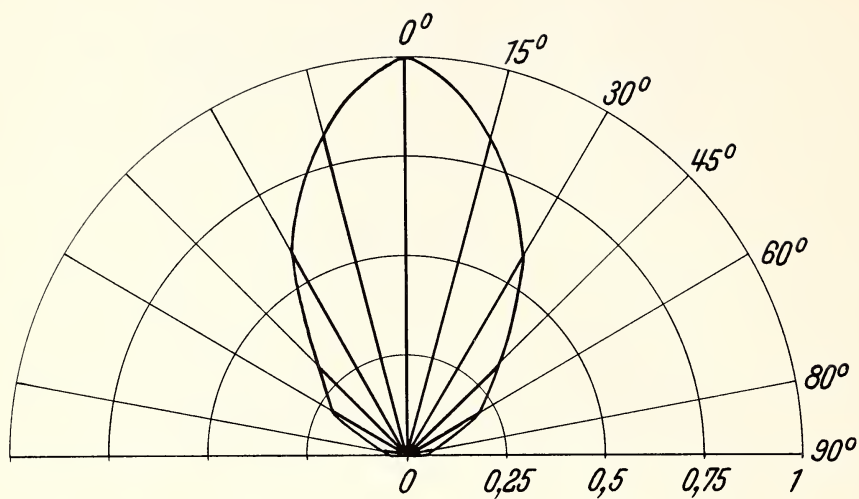


Fig. 4

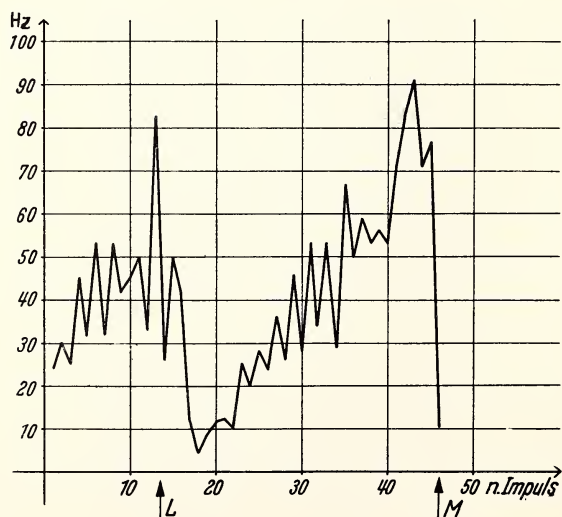


Fig. 5

signals in Megaderma lyra. The pulses are very weak and the animals do not produce regular pulses when held in the hand. Finally, the relative position of microphone and bat must be exactly the same in subsequent measurements. Slight turns of the bat's head cause great differences in the intensity picked up by the microphone because of the focusing effect (see below). By training the bats and using a special experimental arrangement, these difficulties were overcome. We succeeded in obtaining exact measurements of the sound pressure of the signals even in free-flying bats. The highest values of sound pressure at a distance of 6 - 15 cm from the head of the bat were as low as 1 - 1,6 dyn/cm². Megaderma lyra thus merits the title of "whispering" bat. NOVIČK (1958) has given higher values (24 - 58 dyn/cm² at a distance of 7 cm) for the same species. We never obtained values in that range, and believe NOVIČK's estimates too high.

d) focusing effect

Megadermatid bats emit their orientation signals through the nasal pathway as do horseshoe bats (MÖHRES and KULZER, 1957). Earlier experiments had already shown that this kind of emission implied narrow beaming of sound energy. We were able to measure the degree of this focusing effect. As in the above-mentioned experiments, the sound intensity was measured in free-flying bats which were trained to fly on a fixed route to a fixed goal. The position of the animal at the moment of measurement was controlled by photocells. Under these experimental conditions orientation signals are produced with sufficient constancy so that successive measurements of sound pressure at equal distance from but at varying angles to flight direction, gave reliable results. The graph of Fig. 4 shows the directional pattern of sound emission in Megaderma lyra. From the curve it is evident that the beam of sound emitted by the orientating bat is concentrated into a rather narrow bundle. The focusing effect is not as complete as in horseshoe bats (1/2 intensity



Fig. 6

at 35° instead of 23° along the middle line of the head), but it may help to make the sonar of Megaderma carry over a longer distance in spite of the extremely low intensity of the signals.

e) repetition rate

Orientation signals of Megaderma lyra are generally produced in groups or sequences of short or long duration, separated from each other by silent intervals. Two types of sequences may be distinguished: longer sequences with low pulse repetition rate, and sequences with a high repetition and short total duration. High repetition rate sequences are characteristic of bats because their attention is attracted by special objects or excited by general alarm. In such situations, repetition rate varies within an average range of 38-52 pulses/sec for short periods, even rising to 300 or more. If the bat is not alarmed, and its interest in the surroundings has a more routine character, repetition rate is as low as 16-18 pulses/sec. Comparable variation in repetition rate is found in flying bats. In flight, repetition rate is generally higher than in resting position. Fig. 5 demonstrates the variation of repetition rate of bats in approaching an obstacle L and a goal M. In the approach phase the repetition rate rises from about 30 to 57 pulses/sec. At the moment the obstacle (wire grid) is passed, there is a steep decline in the rate to 13, followed by a new rise to about 67 at the feeding place (M) just at the moment before snapping the food. It may be mentioned that in the approach phase the pulses usually appear as twins. Whether this has a functional meaning or not we do not yet know.

2. Efficiency of ultrasonic orientation in Megaderma lyra

Examining the very low intensity of the orientation signals of Megaderma lyra, one would expect the efficiency of their ultrasonic orientation system to be

rather poor. However, daily observation of the flying bats soon showed that this was not true. Placing grids of wire across the bats' pathways proved to be a good method of checking the efficiency of their sonar systems. The bats were trained to pass different grid arrangements placed between a fixed resting point and the feeding place. In a first series of experiments we used grids made of vertical wires of decreasing diameter. In a second series we worked with horizontal wires. Both these arrangements proved to present serious disadvantages. The strong bats did not pay enough attention to the wires because their flight was not much impeded, even when they bumped against the wires. Therefore, in a third series of experiments we used a square grid built of horizontal and vertical wires. The meshes of this square net had a width of no more than 14 cm. Only the results of the third series of experiments will be reported here.

Megaderma lyra (wing-span 38-42 cm) could pass the square grid only by folding its wings close to its body. It was expected that the difficulty of passing this narrow net would terrify the animals, and that a long training period would be necessary. The contrary proved to be true. The bats passed through the net without hesitation and with great skill. Their usual behaviour was to dash through the grid like missiles (Fig. 6).

The grid, fitted with wire of 150 μ diameter, caused 3 bats of one group which made 86 starts to turn back only 15 times. Of 142 passages, 103 were perfect with no touching of the wires. Megaderma lyra, behaving far above random expectation, even avoided wires of 80 μ . Finally wires of no more than 60 μ were used, and then the bats began to tear the thin wires more and more in passing through the net. Being so thin, nylon wires may easily be torn, and do not represent a real obstacle. In spite of this, there were 14 perfect

passages out of 78 with no wire-touching. The behaviour of the bats approaching the net made clear that they could recognize the wires even if they tore them. In any case, the ability of Megaderma to detect very thin wires proved to be much better than in most other species of bats. In this report, Megaderma can be compared only with horseshoe bats (SCHNEIDER and MÖHRES, 1960).

We cannot make definite statements yet about the distance range within which the sonar system of Megaderma lyra is efficient. From the change in repetition rate in approaching objects one might conclude that the system would not carry over distances longer than 50-100 cm. This conclusion may not be valid because the bats were trained, so preceeding orientational experience might have influenced their behaviour. From other observations made the real operating range seems to extend to a distance of 2-3 m. This is a very large range in view of the extremely low intensity of the signals, but this question needs further study in other bats as well as in Megaderma lyra.

Within certain limits our results may be regarded as representative for the whole Megadermatidae family, which must be regarded as having high functional specialization. These "whispering" bats reveal a sonar system of astonishingly high efficiency. One feels tempted to say that this is efficiency in spite of low intensity signals. However, perhaps the low intensity of the orientation signals is a special adaptation to the particular hunting habits of Megadermatid bats and to the special prey they live on. Perhaps weak signals do not alert and alarm the prey (mice, resting bats, birds, geckoes or tree-frogs) before it can be caught by the hovering Megadermatid bat.

A concluding remark may be made in reference to the role of optical orientation in Megadermatid bats. These bats have relatively large eyes and evidently make use of them, but the eyes cannot replace the sonar system. Optical orientation fails to secure navigation if ultrasonic orientation is rendered impossible.

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ABSTRACT

For two years we have kept a group of Indian bats, Megaderma lyra, in our laboratory, and have been able to study the ultrasonic orientation of one member of the Megadermatidae family in detail.

Megaderma lyra's sonar system uses extremely short sound pulses of very low intensity consisting of only a few unmodulated harmonic frequencies. The most intense frequencies are 58.5 and 78.5 kc/sec, respectively, the intensity relation of these two principal frequencies being variable. Pulse duration in resting bats averages 0.67 m/sec. During flight longer pulses averaging 1.18 m/sec are used. When approaching an object the pulses get continuously shorter, averaging 0.7 m/sec. Sound pressure of orientation sounds is very low even in flight. Maximal sound pressure in flight at a distance of 6 to 10 cm from the sound emitting nostrils was measured to be 80 to 85 dB ($2-3.2 \text{ dyn/cm}^2$). The nose-leaf function as a focusing device which concentrates the sound energy into a narrow bundle, the intensity gradation of which can be measured in flying animals. At an angle of 35° from the middle line of the head sound pressure is already reduced by 50 %. Repetition rate is very variable. When approaching an object in flight, the repetition rate goes up to an average value of 70 per second, while simultaneously pulses are shortened and twin pulses may appear. Performance and efficiency of ultrasonic orientation is excellent in spite of extremely weak orientation sounds. Megaderma lyra can detect wires as thin as 60 in diameter. The eyes of this bat and other members of the same family are much bigger than in most other bats. They play a certain role in orientation, but cannot assure navigation if ultrasonic orientation is rendered impossible.

THE ROLE OF SPACIAL MEMORY IN THE ORIENTATION

by

G. NEUWEILER and F.P. MÖHRES

During the experiments reported in the previous paper (F.P. Möhres and G. Neuweiler) we made some puzzling observations. In the same experimental set-up our trained bats (Megaderma lyra) used some of the 70 identical squares of the mesh-net obstacle more frequently for flying through than they used other ones. There may be two reasons for this preference of certain positions:

- 1) the bats simply tried to fly through the door-frame as far from the door-posts as possible and therefore had to pass through the squares in the middle of the net only. This was not the case.
- 2) Then the only other reason for spatial preference may be: The bat remembers the position of the square it previously passed through and continues to fly through that particular hole. If it be so, this spatial memory should be detected by the frequency the bats flew through a particular square of our meshnet obstacle.

During ten days we recorded the position of the square a bat passed through in every flight and also noted, if the bat passed untouched (+), touched or even hit the files (-). Without using any spatial memory, the per chance level of flights through each square would be 2.77 %, taken in consideration already that the bats rarely used the border rows.

The results are given in Fig. 1: Each rectangular meshnet is a true-to-scale graph of the actual obstacle fitted into the door-frame. Each square is numbered vertically from left to right and horizontally from top to bottom (e.g. square no. 4/9 means the ninth square from top in the fourth vertical row). The figures within the square give the percentage of flights through that particular square out of the total number of passes within the denoted period. The flights to the feeding place were plotted separately (black figures) from the return flights to the roosting place (dotted figures), because the animals behaved differently in the two situations.

Bat no. 3 mostly used the second and third vertical row for flying to the feeding place and clearly the ninth horizontal square by preferred 18.7 and 10.5 % and the tenth horizontal one of the second row by 11.5 %. It very rarely entered through the fourth row but almost exclusively used just this one for returning to the roosting place, the lower preferring squares no. 10, 11 and 12 in 55 % of all returning flights. So - as in the other bats tested - it very rarely flew out through the same square which it used for flying in. Though there were two distinct and clearly separated passing areas in bat no. 3, the position of all used squares spread rather widely compared with those of the other two bats and conspicuously enough this bat only scored a low percentage of correct flights, i.e. untouched passes: 39.7 % correct among the more widely spread in-flights and 52.7 % among the more confined returning flights.

Bat no. 2 gave more clear cut results, distinctly sticking to certain single squares for passing through. For flying in it used the third preferred vertical row and clearly the sixth horizontal square. While returning it invariably passed through the neighbouring square of the second row. The still high percentage of flights through the squares just above the most frequented ones results from a shift of preference after three days of training. The squares used are restricted to a much smaller area than in the previously reported bat, and the percentage of correct flights rose markedly by 11 and 20 %.

The most striking result was obtained from bat no. 1 which used in 95 % of all flights one single square (No. 4/13) for flying in, and in 97 % the square no. 2/13 for flying back. This animal most stubbornly using particular holes also turned out to be the most skillful flier. It scored 65.7 and 79.1 % correct flights. It flew through the meshnet obstacle at utmost speed right from the starting place, and yet only rarely hit the wires of the invariably used squares no. 4/13 and 2/13. In all our experiments the number of correct flights rose as soon as a bat began to use only a restricted area or a single square for passing through.

From the observations reported so far we may conclude:

- 1) Bats use spatial memory for obstacle avoidance, or generally speaking for reorientation.
- 2) There is a positive correlation between the ability to avoid obstacles in a familiar situation and the use of spatial memory in ultrasonic orientation.

But how does refined spatial memory work in bats? If one shifts the meshnet obstacle to one side, do the bats follow this shift according to the ultrasonic information, or will they be lead to the now-barred previously used positions by spatial memory? When spatial memory gets the better of ultrasonic orientation, the number of hits should increase after a shift of the meshnet.

After three days of standard training we shifted the net within the frame by 8 cm upwards and to the left. In the graph of Fig. 2 the percentage of correct flights is plotted for each daily experimental sequence. The lower line shows the returning flights, the dotted line the flights into the feeding room of bat no. 1. After shifting the meshnet by 8 cm the percentage of correct flights significantly dropped by more than 30 %. But within the next few days the bat regained its former skillfulness. After the next shift of 4 cm backwards towards the original position, the bat in nearly all of the returning flights bumped against the wires at full speed, whereas while flying in it navigated more carefully and still scored 68 % correct flights as compared to 94 % before shifting. After the following shifts of 2 cm only, the bat rarely touched the wires while flying in. It obviously was lead by its immediate ultrasonic information, and not by memory. Whereas while flying back to the roosting place, the animal became seriously desorientated after each shift and learned to pass through after two or more days of training. The complete desorientation after a shift of 2 cm only, indicates that the position of the previously passed square is remembered

by an accuracy of at least 2 cm.

The great difference between flights into the feeding room and flights back to the roosting place results from the behavioral attitude of this bat to the experimental situation: it always tended to remain as shortly as possible in the unfamiliar room where it got its mealworm. Therefore it always flew carefully from the familiar roosting room to the strange feeding room and aimed as quickly as possible back to the roosting place as soon as it had grasped its insect. During these hasty returning flights the bat obviously relies on spatial memory, and shunts its immediate sensory input.

When memory works in bats with an accuracy of 2 cm, one might also suspect that it perseveres over a long temporal period. We therefore stopped the training of obstacle avoidance for 6 weeks. When we started the experiments again, all three bats still used the same vertical rows for passing through the obstacle that they had used before the break. But the horizontal position had moved by one to four squares (Fig. 3 the shaded square marks the formerly most frequently used square). After this short interception of one week's training, we again stopped the experiments for another 6 weeks (Fig. 4). After this second break the bats had great difficulty to pass through the obstacle and flew into the feeding room very reluctantly. The position of the most frequently used square now had shifted not only horizontally but also vertically. In the first days of retraining the bats in nearly every flight passed through another square and very frequently hit the wires. But in the second halve of the

week the flight pattern stabilized, the bats began to stick to particular squares for passing and consequently the number of correct flights increased markedly. This is best seen in bat no. 1 (Fig. 5). In the first two days the bat flew towards the lower squares which it had used 6 weeks before, but now it stopped immediately in front of the meshnet, slowly hovered upwards along the fourth and fifth row, and finally entered by the upmost square, invariably hitting the wires. It hastily flew back through any square of the first and second row. On the third day it began to prefer the lower squares, and in the following days mostly used square no. 5/12 for flying in and square 1/12 for returning. As soon as the bat began to consistently pass through a particular square, the number of correct flights immediately increased by 16 %. Apparently when pretraining time is short, after a break of 6 weeks the bats remember only vaguely the position of previously used passes.

In all the experiments so far reported sensory information was already available to the bat. But what happens if one removes the wires, thus blocking any ultrasonic perception of the squares? We trained another group of three bats to fly through a cleft, 42 cm wide, split vertically by a wire of 1.2 mm diameter into a right and a left halve. The per chance level to hit this wire while passing through the gap was 47 %. All bats quickly learned to avoid the middle wire by folding in their wings. After four days of training we removed the wire obstacle and put a light-barrier at the position of the former obstacle. Each time this sham-obstacle was crossed even by the tip of a wing we got a deflection on a CRO - screen to which the photocell was connected.

Since this imaginary obstacle could neither be seen nor echo-located by the bat we could control for how long the bat considered the no more existing obstacle still to be there. Again the results differed among different specimens and between flights into and back from the feeding room. In bat no. 1 (Fig.6) the number of hits - i.e. of shading the lightbeam - by the spread wing increased steeply and immediatly whereas bat no. 2 while flying in for 3 days still carefully folded its wings when passing through the wide gap in order to avoid an obstacle which only existed in his memory. Bat no. 3 for two days continued to respect the sham obstacle while returning, and even used the narrower passway of the imaginarily divided gap. After we divided the gap again by a real wire the number of hits promptly dropped down to near zero. After a training period of six days we again replaced it by the lightbeam. After this longer training period we got more clear cut results: In four successive days bat no. 1 still folded its wings to avoid hitting a non-existent obstacle, whereas bat no. 2 behaved normally and flew across the light barrier at will already on the second day. A most striking fact was that bat no. 3 in 14 returning flights not even once shaded the lightbeam by its wings.

These experiments show that the position of obstacles which have been removed days before are still remembered by bats, so they continue to avoid them as if they were still in place. Apparently bats rely more on spatial memory than on immediate sensory data gained by echolocation for orientation while flying in an already well-known surrounding.

Explanation of the figures

Each grid is a depiction in a reduced scale of the meshnet obstacle used in the experiments.

Where not otherwise specified the figures within the squares give the percentage of flights through that particular square as derived from the total number of flights in the denoted experimental period.

Solid figures: Percentage of flights into the feeding room.

Dotted figures: Percentage of flights returning to the roosting room.

Herflug: Number of flights into the feeding room.

Hinflug: Number of flights returning to the roosting room.

% ri: Percentage of correct flights.

Tier: Animal no.

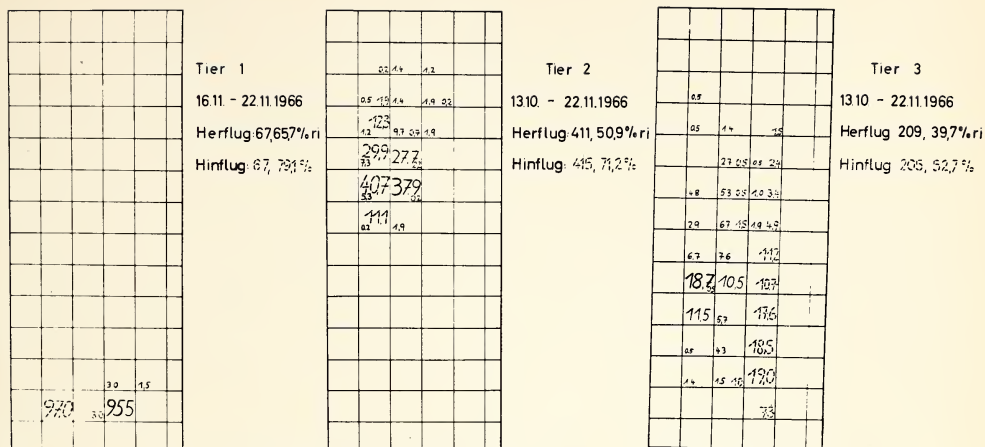


Fig. 1: Position preference in obstacle avoidance in Megaderma lyra.

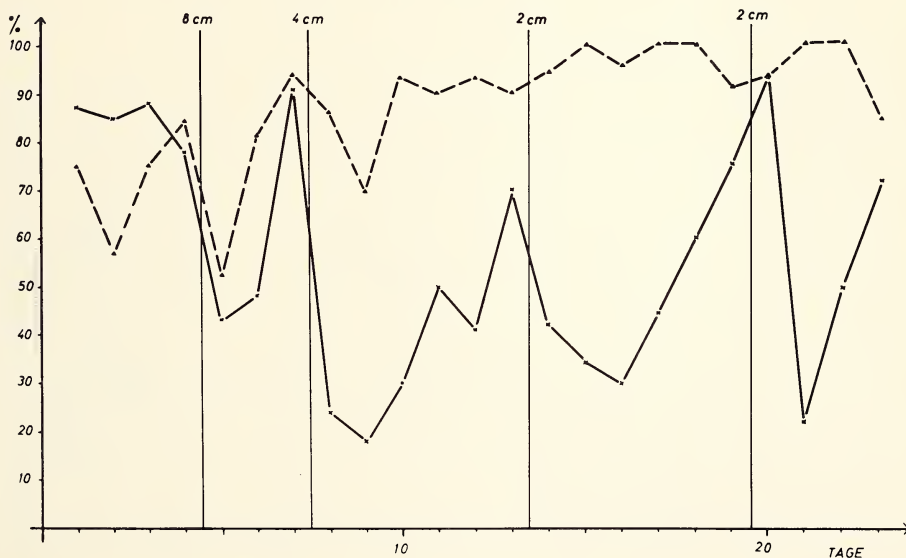


Fig. 2: Passage through the shifted meshnet obstacles of bat no. 1
 Abscissa: successive experimental days (Tage = days).
 Ordinate: % of correct flights
 Dotted line: flights into the feeding room
 Solid line: returning flights
 Vertical bars mark the time when the meshnet was shifted
 by the denoted number of cm.

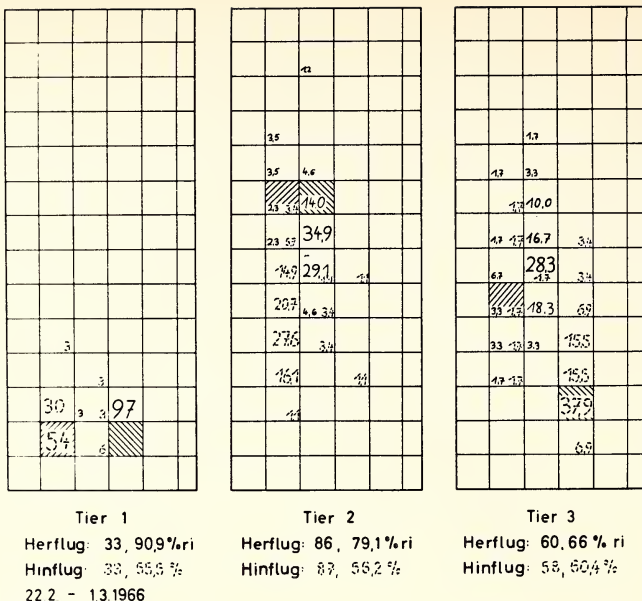


Fig. 3: Position preference after a 6-week break of training.
 Shaded squares: most frequently used squares before the break.

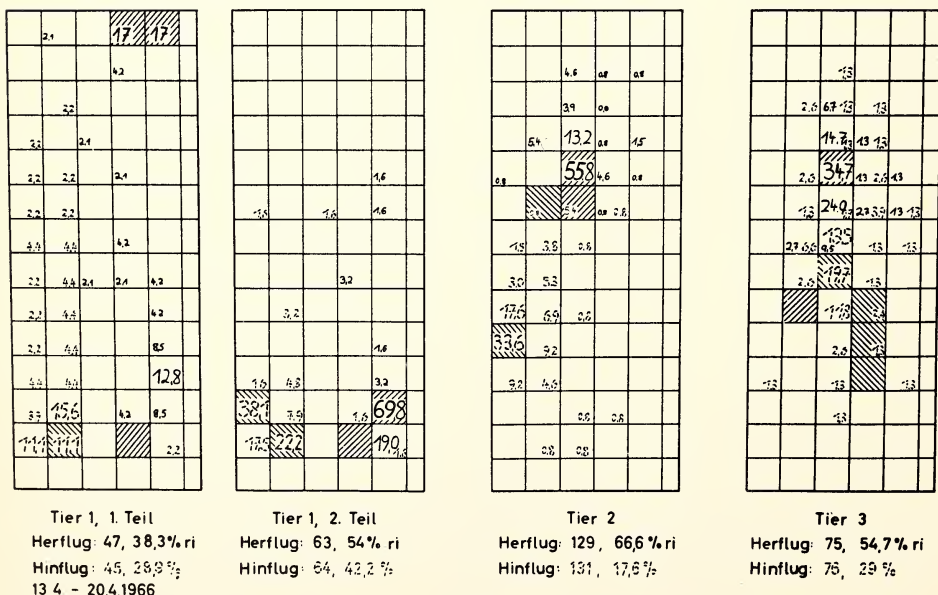
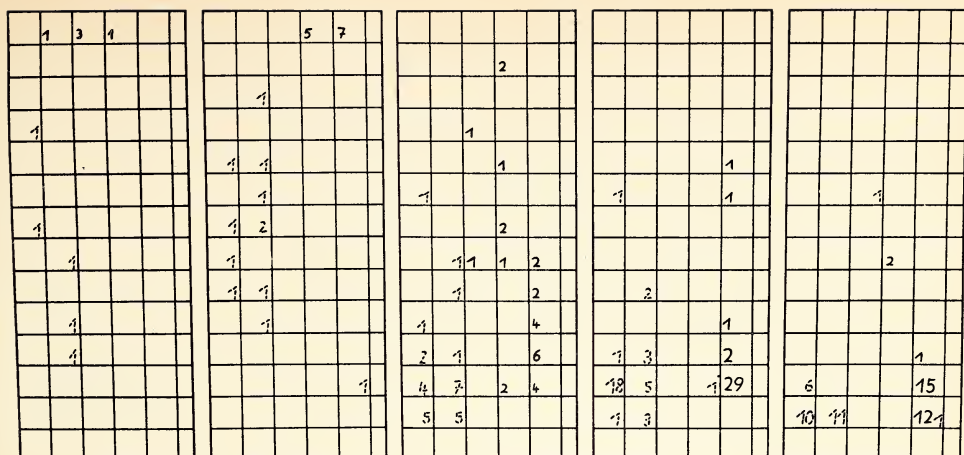


Fig. 4: Position preference after another 6-week break of training.
 Shaded squares: most frequently used squares before the break.

1. Teil: position preference of bat no. 1 in the first three days of retraining.
2. Teil: position preference of bat no. 1 in the following 3 days of retraining.



Tier 1, 14.4. - 20.4.1966, — Herflug, ---Hinflug

Fig. 5: Position preference in obstacle avoidance in bat no. 1 in the first successive 5 days of retraining. Each grid gives the result of one day.

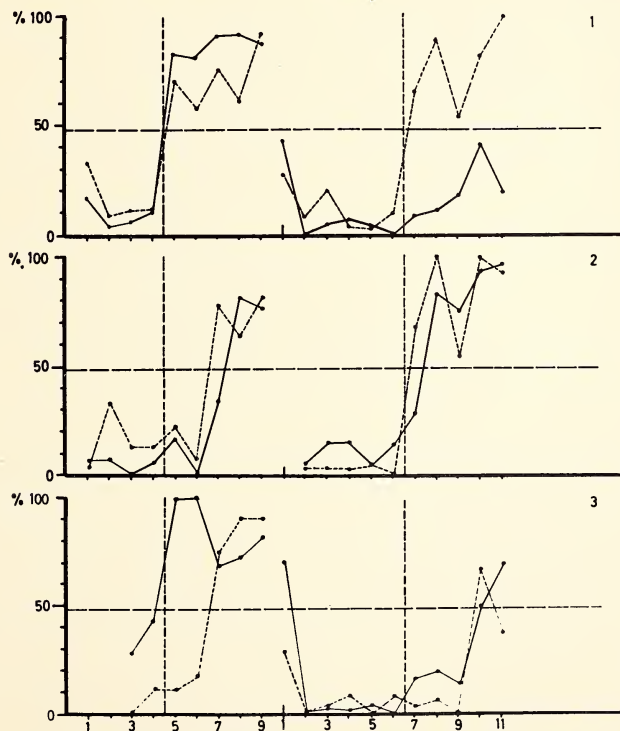


Fig. 6: Temporal memory of the position of an obstacle. Right upper figure marks the bat no.
 Abscissa: successive experimental days
 Ordinate: % of hits against the obstacle or crossing the light-barrier respectively
 Dotted horizontal line: per chance level of hits
 Dotted vertical line: replacement of the wire obstacles by a light-barrier
 Solid curve: flights into the feeding room
 Dotted curve: returning flights

ABSTRACT

In obstacle avoidance experiments evidence shows that the bat Megaderma lyra Geoffr. uses spatial memory for reorientation. There is a positive correlation between the ability to avoid fixed obstacles and the degree to which a bat makes use of its spatial memory. The position of narrow squares for passing into another room is remembered by an accuracy of 2 cm. Even small obstacles when removed are still remembered for days, and the bats continue to avoid the position of the non-existent obstacles in flight.

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UNE MÉTHODE D'ANALYSE FRÉQUENTIELLE DE SIGNAUX COMPLEXES ET SON APPLICATION AU CAS DE SIGNAUX BIOLOGIQUES D'ÉCHOLOCATION

par
F. AUDOUIN

INTRODUCTION

On connaît dans le domaine radar l'importance de l'analyse fréquentielle appliquée à la détection d'un signal dans le bruit ou le clutter. Deux grandes classes de procédés sont possibles : par filtrage au moyen de filtres discrets ou par analyse fréquentielle suivant des méthodes basées sur l'analyse de Fourier. On se propose, après avoir discuté de divers schémas possibles, de décrire une méthode purement numérique à la fois classique et très générale : évaluation des composantes spectrales du signal par transformation de Fourier de sa fonction d'autocorrélation. Ceci amènera à discuter des problèmes d'échantillonnage et de codage sous forme numérique des données pour l'utilisation par le calculateur.

Cette étude est entreprise sous l'égide de la Direction des Recherches et Moyens d'Essais (PARIS) à qui nous exprimons notre gratitude pour son soutien.

I - ANALYSE FREQUENTIELLE PAR FILTRES - DISCUSSION

Une première classe de procédés est l'analyse par filtrage, par exemple par une batterie de filtres couvrant toute la gamme de fréquences à analyser. En radar ce procédé est utilisé par exemple pour mesurer la vitesse radiale (liée au décalage Doppler) d'un mobile.

Dans ce cas représenté en figure 1, le signal de durée totale T attaque n filtres en parallèle, de bande passante individuelle $B = 1/T$, dont les sorties sont détectées et explorées par un système de lecture.

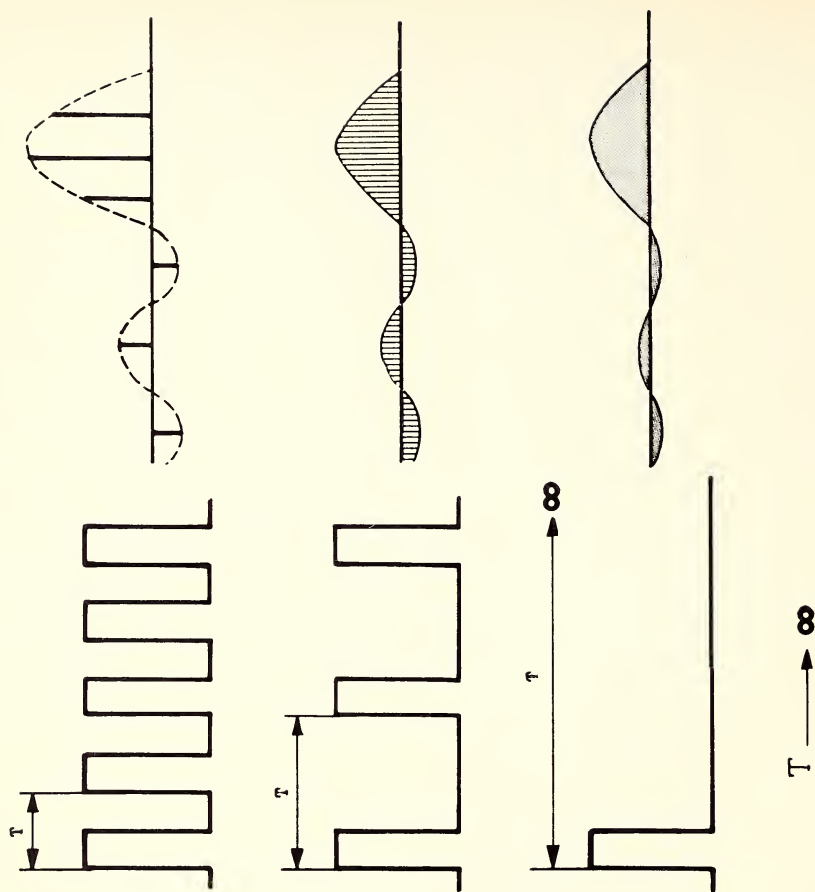


Fig. 2 - Intégrale de FOURIER (Spectre continu)

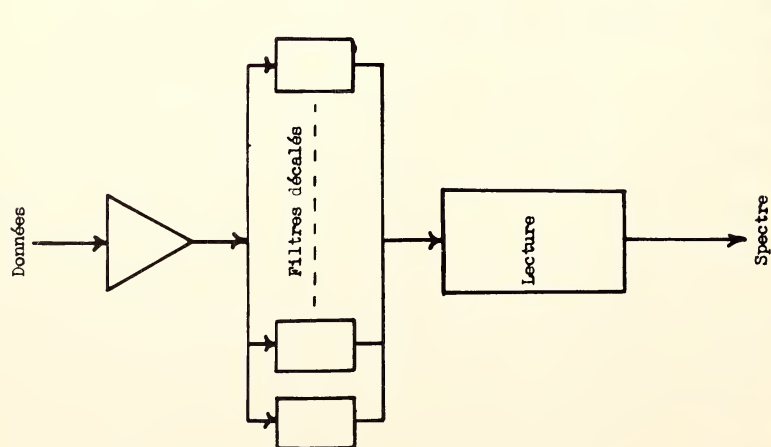
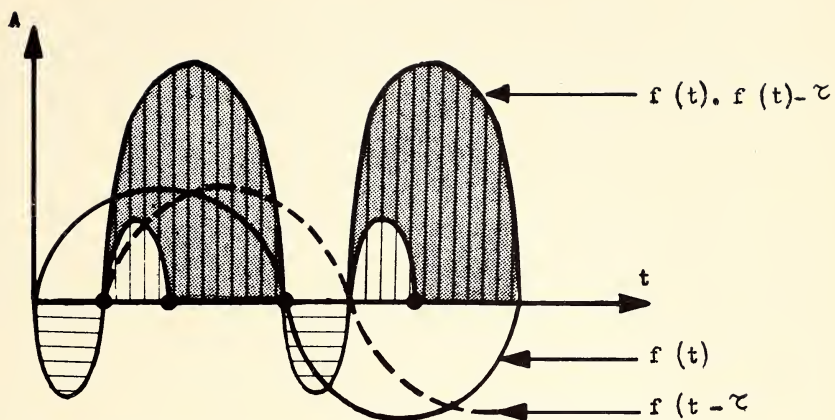
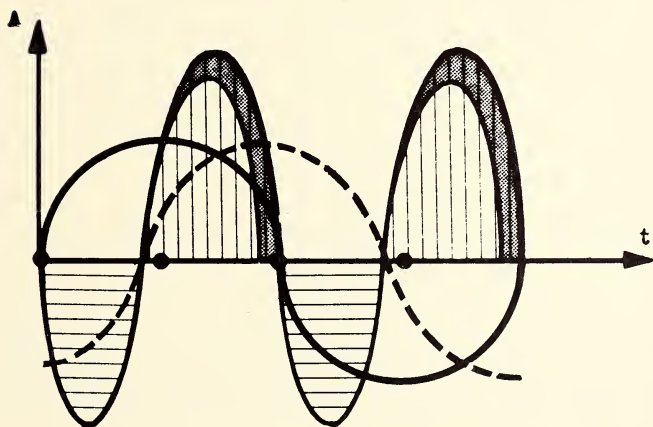


Fig. 1 - ANALYSE FREQUENTIELLE PAR FILTRAGE



a) Corrélation forte



b) corrélation faible

Fig. 3 - FONCTION D'AUTOCORRELATION-INTERPRETATION

On obtient par cette lecture les caractéristiques fréquentielles du signal. Mais si l'on considère par exemple un signal de durée 1 msec. on définit ipso-facto la largeur de bande des filtres à 1 Kc (la fréquence ne pourra être mieux déterminée). Pour un signal dont les fréquences s'étendraient jusqu'à 100 kcs, il faudrait une centaine de filtres, ce qui représente un équipement complexe et onéreux.

Lorsqu'il n'y a pas nécessité de travailler un temps réel, on peut utiliser un filtre unique exploré par changement de fréquence. Il faut passer le signal plusieurs fois consécutives, ce qui n'est pas très gênant, mais des intermodulations (et donc des fréquences parasites) sont inévitablement créées dans le modulateur analogique, qui ne peut pas être parfait.

II - ANALYSE FREQUENTIELLE PAR ANALYSE DE FOURIER

On sait par cette analyse reconnaître, dans une fonction périodique, un fondamental et des harmoniques. C'est à dire que l'amplitude de la fonction signal s'écrit :

$$f(t) = \sum_k A_k \sin(k \omega t + \varphi_k)$$

où $\omega = 2\pi/T$ est le fondamental, ce qui correspond à un spectre discontinu (spectre de raies).

Si la fonction n'est plus périodique et devient quelconque, selon Fourier, cette fonction peut se représenter par une intégrale de la forme :

$$f(t) = \int_0^\infty A(\omega) \sin(\omega t + \varphi) d\omega$$

qui généralise la sommation discontinue utilisée dans le cas périodique et qui correspond à un spectre continu. (Fig. 2)

En fait, on utilise pour déterminer ce spectre un artifice, le seul vraiment praticable pour l'étude d'un signal non périodique un peu complexe. Il s'agit de calculer d'abord la fonction d'autocorrélation du signal ou

autocovariance, puis de déterminer le spectre de fréquence par transformation de Fourier de cette autocovariance.

De façon quantitative, la "corrélation" désigne un certain degré de correspondance relative entre 2 ensembles de données (une corrélation de 75 % par exemple). C'est la mesure d'un rapport de ce type qui est réalisée dans l'extraction d'un signal radar par corrélation, les échos multiples de bruit environnant correspondant au contraire à des signaux totalement décorrélés.

La corrélation a une interprétation physique connue si l'on mélange les signaux $f_1(t)$ et $f_2(t)$ en réalisant la somme :

$$F(t) = f_1(t) + f_2(t)$$

l'énergie moyenne est :

$$\overline{F(t)^2} = \overline{f_1(t)^2} + \overline{f_2(t)^2} + 2 \overline{f_1(t) f_2(t)}$$

Les deux premiers termes représentent l'énergie propre à chaque signal, le 3e terme est une énergie d'interaction .

En d'autres termes, soit 2 signaux sinusoïdaux identiques décalés de τ et soit la courbe représentative (C) du terme produit $f(t) \cdot f(t - \tau)$. Sa moyenne est donnée par la somme algébrique des aires $\Sigma A_{(+)} - \Sigma A_{(-)}$ (zone ombrée). Comme on s'y attend, dans le cas de la figure 3a où le retard τ est petit la corrélation est forte. Elle est nulle si $f(t)$ et $f(t - \tau)$ sont en quadrature. La situation donnée en figure 3b est voisine de ce cas.

La fonction d'autocorrélation est le terme d'interaction obtenu en comparant le signal $f(t)$ avec lui-même à 2 instants $t - \tau$ et t et en prenant la moyenne de leur produit :

$$\rho(\tau) = \overline{f(t) f(t - \tau)} = \frac{1}{T} \int_0^T f(t) f(t - \tau) dt$$

Considérant alors plus précisément le sens énergétique de la fonction d'autocorrélation $\rho(\tau)$, et si $\rho(\tau)$ a une transformée de Fourier continue $A(\nu)$:

$$\rho(\tau) = 2 \int_0^{\infty} A(\nu) \cos 2\pi \nu \tau d\nu$$

Par inversion, on obtient la densité spectrale du signal original :

$$A(\nu) = 2 \int_0^{\infty} \rho(\tau) \cos 2\pi \nu \tau d\tau$$

C'est à dire que $A(\nu) d\nu$ représente l'énergie du signal $f(t)$ qui correspond à la bande de fréquence $(\nu, \nu + d\nu)$.

L'organigramme correspondant à ce calcul est donné en fig. 4 (le programme est rédigé en FORTRAN IV) %.

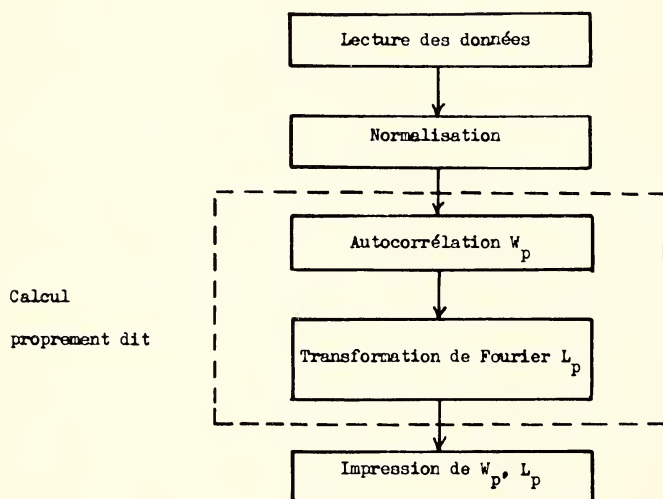


Fig. 4 - ORGANIGRAMME DE CALCUL

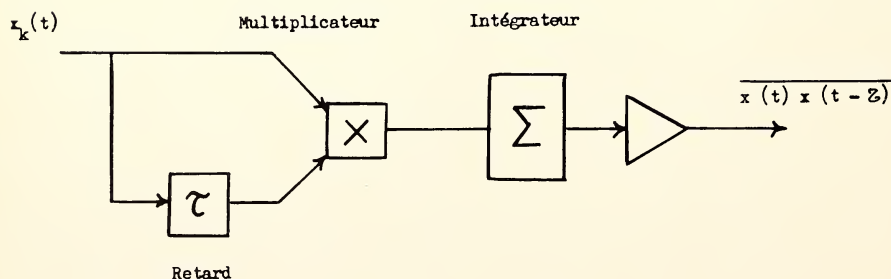


Fig. 5 - CORRELATEUR

Ces opérations peuvent être réalisées de façon analogique. D. A. CALHANDER - M.I.T. - a ainsi effectué des calculs d'autocorrélation sur des signaux de chauve-souris qui lui avaient donné de bons renseignements sur leur type de sonar. Plus précisément CALHANDER utilise un circuit analogique du type corrélateur (figure 5) pour calculer la fonction signal ou diagramme d'ambiguïté ; le signal reçu étant affecté, par rapport au signal émis d'un retard τ et d'une dérive Doppler α , on effectue ensuite la convolution de ces 2 signaux, c'est à dire multiplication et intégration. La simulation du retard τ entre les signaux sur 2 pistes est obtenu en retardant ou avançant l'une des 2 têtes de lecture amovibles. La dérive Doppler α , en tant que compression ou expansion de l'axe du temps, est simulée par de petits accroissements de la vitesse du reproducteur de bandes ou par l'intermédiaire d'une dérive d'oscillateur.

Plusieurs sources d'erreurs interviennent :

- erreurs sur la fonction elle-même : à l'origine, il y a les erreurs d'enregistrements dues aux microphones et aux échos environnants et une variation d'amplitude éventuelle à la lecture de la bande.
- erreurs sur la dérive Doppler : les plus grandes dérives enregistrées sont de 10 m/sec. ce qui correspond à une variation de 6 % de la fréquence du signal de la chauve-souris. A la lecture de bandes, les erreurs sont dues au flutter et aux dérives d'oscillateur. Selon CALHANDER, l'erreur globale correspondante en fréquence donne une erreur sur la vitesse de 0,9 m/sec. On trouve alors pour un diagramme d'ambiguïté s'étalant de -10 m/sec. à +10 m/sec, une erreur de position de 4,4 %.
- erreurs dues au multiplicateur : on sait que la limite de précision absolue d'un organe élémentaire de machine analogique n'est pas meilleure que le millième de l'échelle totale. Un multiplicateur analogique ne peut donc fournir un résultat qu'à quelques pour mille. D'autre part, le produit des 2 ondes décalées introduit, entre fréquences sommes et différences, une intermodulation en sortie. On compte finalement sur 0,4 % d'erreur en fréquence due au multiplicateur.

- erreur d'intégration : la présence inévitable de bruits dans les amplificateurs et de non linéarités entraîne nécessairement des dérives des intégrateurs.

En conclusion, CALHANDER donne l'estimation d'erreurs suivante :

- 5 % en amplitude du signal maximum, 0,5 % de l'échelle totale pour la durée de retard τ , et 4,4 % sur la dérive Doppler.

Il est souhaitable de réduire ces taux d'erreurs le plus possible et cela, le traitement par calculatrice arithmétique nous le permet. D'où la méthode d'analyse fréquentielle purement numérique proposée ici.

Mais pour effectuer des calculs numériques, et non plus analogiques, il faut tout d'abord transformer le signal originel en une série de nombres. C'est le rôle de l'échantillonnage et du codage.

III - ECHANTILLONNAGE

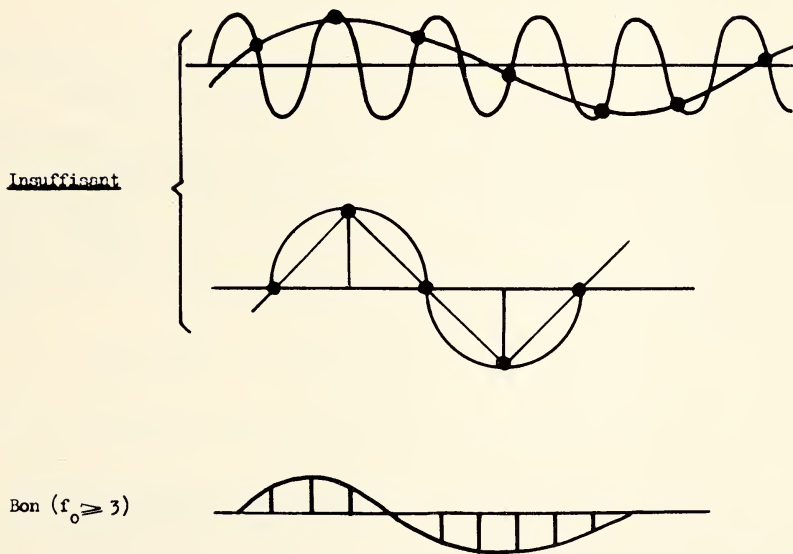
L'échantillonnage consiste à remplacer, en une série de points déterminés, une fonction mesurée pour une tension de même valeur qui reste constante d'un point d'échantillonnage au suivant. La densité des points d'échantillonnage nécessaires pour bien reconnaître $f(t)$ dépend de la vitesse de variation de ce signal. Théoriquement, si $f(t)$ n'a pas de fréquences supérieures à F , il est complètement connu par échantillonnage à la fréquence $f_0 = 2 F$.

En fait, on voit sur la figure 6, qu'un échantillonnage insuffisant peut créer des ambiguïtés, par exemple :

- Impossibilité d'identifier une sinusoïde du fait d'un déphasage malencontreux entre signal à échantillonner et figure d'échantillonnage.
- Possibilité de confusion de la fréquence analysée avec une fréquence sous harmonique.



a) Définition



b) Taux d'échantillonnage

Fig. 6 - ÉCHANTILLONNAGE

Tout échantillonnage est caractérisé par l'instant de prélèvement et la précision de mesure (en ordonnée) de l'échantillon. Cette mesure est donc entachée d'une double cause d'erreur sur le temps et sur l'amplitude. On doit se demander en ce sens quel est le degré d'approximation obtenu quand on remplace ainsi la courbe du signal par une fonction en escalier. Si l'échantillonnage est le plus souvent régulier, l'allure du signal peut nécessiter parfois de faire varier la fréquence d'échantillonnage. Le choix de cette fréquence est fondamental du point de vue traitement numérique par un calculateur digital. Si elle est trop petite, il y a perte d'information ; si elle est trop grande, il y a encombrement inutile des mémoires sans amélioration des performances du système.

En pratique, pour une reproduction assez fidèle, c'est insuffisant et l'on adopte en général $3 F < f_0 < 5 F$.

Il est intéressant de constater la conformité de cette conclusion avec celle de Moles sur la reconnaissance de structures par le cerveau. Etudiant la perception des structures visuelles ou sonores chez l'homme, bien que la sensation de périodicité nécessaire à identifier une structure soit limitée par son délai de perception, cet auteur estime qu'il suffirait qu'un événement se répète 3 à 4 fois de façon isochrone pour que l'esprit du sujet soit mis en attente de l'événement suivant. L'établissement de l'autocorrélation se situerait entre 3 et 5 périodes.

CONCLUSION

La méthode numérique d'analyse fréquentielle proposée ici doit permettre une analyse fine de la structure des "clics" d'écholocalisation, plus précise que les méthodes analogiques. Cette méthode numérique est très générale et applicable à des signaux d'écholocalisation quelconque.

En raison de l'efficacité de la localisation par écho acoustique chez les dauphins et les chauve-souris, il serait souhaitable de voir par cette analyse si leurs caractéristiques opérationnelles ne correspondent pas à une structure spécifique de ces signaux.

I - NOTIONS PRELIMINAIRESI - 1 Probabilité - définition de base

Fonction de répartition $F(x)$ d'une v. a. X continue : $F(x) = \Pr(X \leq x)$

Densité de probabilité de X ($F(x)$ dérivable) :

$$dF = p(x) dx = \Pr(x \leq X \leq x + dx)$$

- Moment d'ordre n

$$(\text{moyenne de } x^n) \quad E(X^n) = \begin{cases} \sum_1 x_1^n p_1 & X \text{ discontinue} \\ \int_{-\infty}^{\infty} x^n dF & X \text{ continue} \end{cases}$$

- Moment d'ordre 1 (moyenne de x) : $E(X) = m$

moment centré d'ordre 2 ou variance : $\mu_2 = E[(x - m)^2]$

$$\text{écart type} : \sigma = \sqrt{\mu_2}$$

- Variable réduite

$$X' = (X - m)/\sigma$$

- Fonction caractéristique de la v. a. X

$$\varphi(t) = E(e^{jtx}) = \int e^{jtx} p(x) dx$$

$$e^{jtx} = \cos tx + j \sin tx$$

- Covariance $\text{cov}(X, Y) = E[(X - m_x)(Y - m_y)]$

- Coefficient de corrélation $r = \text{cov}(X, Y) / \sigma_x \sigma_y$

I - 2 Processus aléatoire

Les résultats de mesures sont supposés tirés au sort à chaque instant t_1 . Selon les fig. A1, A2 il existe en t_1 un ensemble de valeurs possibles $x_k(t_1)$ prises par une variable $X_1(t_1)$ avec une certaine probabilité. On définit alors

- une fonction de répartition $F_1 = \Pr(X_1 < x_1)$ à un instant t_1

- une fonction de répartition $F_2 = \Pr(X_1 < x_1 ; X_2 < x_2)$ à 2 instants t_1, t_2

- une covariance $m_{11} = E(x_1 \cdot x_2)$ qui, si X est stationnaire, est une fonction $m_{11} = W(p)$ de $p = t_2 - t_1$ seul.

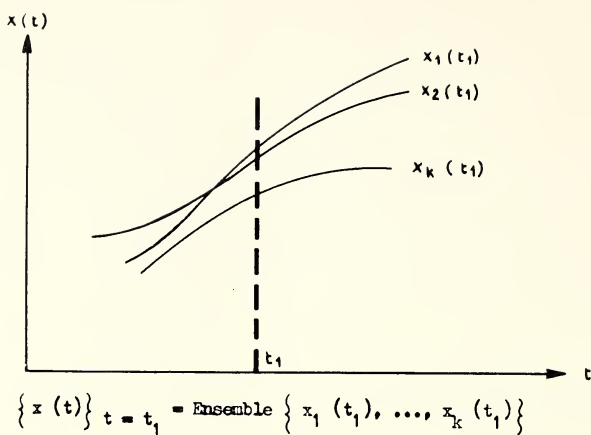
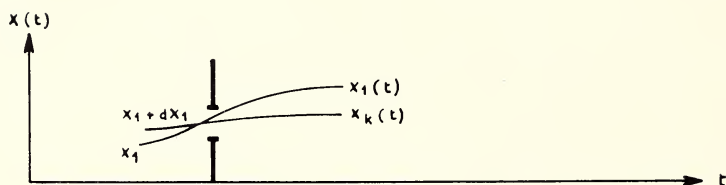
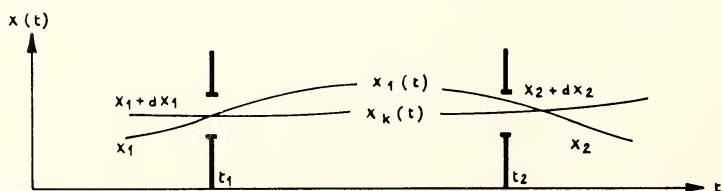


Fig. A1 : Définition d'un processus aléatoire.



Etude à un instant t_1 - Interprétation de $f_1(x_1(t_1))$



Etude à 2 instants t_1, t_2 - Interprétation de $f_2(x_1(t_1), x_2(t_2))$

Fig. A2 : Interprétation géométrique des lois de densité d'un processus aléatoire.

II - AUTOCORRELATION ET ANALYSE SPECTRALE - PRESENTATION DE LA METHODE.

II - 1 Spectre et covariance

Nous connaissons la définition de la covariance $W(p)$ d'un processus stationnaire ou $p = t_2 - t_1$. Une étude plus précise montrerait alors l'analogie entre covariance $W(p)$ et fonction caractéristique p ; on démontre que

$$W(p) = \varphi(p) \cdot W(0) \quad \text{et on sait que}$$

$$\varphi(p) = \int e^{j p \omega} dF_0(\omega)$$

si $F_0(\omega)$ est la fonction de répartition d'une variable.

Si nous posons, $dF = W(0) dF_0$, il vient :

$$W(p) = \int e^{j p \omega} dF(\omega)$$

C'est le théorème de Bockner Kintchine, base de notre calcul.

Si $X(t)$ est aléatoire stationnaire et de covariance continue $W(p)$, on peut écrire

$$W(p) = \int_{-\infty}^{+\infty} e^{j p \omega} dF(\omega)$$

ou F, w est la fonction spectrale de $X(t)$.

Si $F(\omega)$ a une dérivée $F'(\omega) = P(\omega)$ (densité spectrale) on obtient de même :

$$W(p) = \int_{-\infty}^{+\infty} e^{j p \omega} P(\omega) d\omega$$

Physiquement, dans notre cas, le phénomène étudié $X(t)$, non périodique, doit être considéré en raison de sa complexité comme une fonction aléatoire ; cependant, son allure donne suffisamment l'idée de permanence pour le considérer comme stationnaire et le théorème de Bockner-Kintchine est applicable.

En conclusion, entre fonction spectrale et covariance, il y a la même relation qu'entre fonction de répartition et fonction caractéristique : c'est la transformation de Fourier. Finalement on obtient, par cette transformation, la représentation spectrale de $X(t)$ si l'on connaît sa covariance :

$$W(p) = E [x(t) \cdot x(t+p)]$$

II - 2 Méthode de calcul

- On remarque d'abord que :

$$\text{Cov}(X, Y) = E [(X - E(X))(Y - E(Y))] = E(XY) - E(X)E(Y)$$

$$\sigma_X^2 = E(X^2) - (E(X))^2$$

$$r = \text{cov}(X, Y) / \sigma_X \sigma_Y$$

Si x et y désignent 2 échantillons d'une même variable aléatoire $X(t)$: x_i et x_{i+p} , décalées de p intervalles de temps, on obtient l'expression

$$r_p = \text{cov}(X_i, X_{i+p}) / \sigma_{X_i} \sigma_{X_{i+p}} \quad \text{coefficient d'autocorrélation}$$

$$i = 1, 2, N - p$$

en remarquant qu'il n'y a que $N - p$ appariements possibles de x_i, x_{i+p}

- Il y a intérêt à "normaliser" les données sous la forme réduite $(x - m) / \sigma_x$; alors en supposant de plus un écart type σ constant indépendant du domaine d'échantillonnage

$$E(X_i) = E(X_{i+p}) = 0$$

$$\sigma_{X_i} = \sigma_{X_{i+p}} = \sqrt{E(X_i^2)}$$

d'où le coefficient d'autocorrélation réduit

$$r_p = E(X_i X_{i+p}) / E(X_i^2)$$

On considère les $N - p$ échantillons $x_1, x_1 + p$ comme affectés de la même probabilité $1 / (N - p)$. Il vient ainsi :

$$E (x_1^2) = \sum_1 x_1^2 / (N - p) \quad i = 1, 2, \dots, N - p$$

$$W(p) = E (x_1 x_1 + p) = (\sum_1 x_1 x_1 + p) / (N - p) \quad \text{autocovariance}$$

$$r_p = (\sum_1 x_1 x_1 + p) / \sum_1 x_1^2 \quad \text{coefficient d'autocorrélation}$$

Selon le théorème de Bockner Kintchine, nous avons vu que

$$W(p) = \int_{-\infty}^{+\infty} e^{2j\pi fp} P(f) df$$

on obtient $P(f)$ comme transformée inverse de $W(p)$

$$P(f) = \int_{-\infty}^{+\infty} W(p) e^{-2j\pi fp} dp$$

C'est la densité spectrale (contributions des fréquences de f à $f + df$)
En pratique $x(t)$ est réelle, $W(p)$ est fonction paire de p , donc on peut se ramener à une transformation en série de cosinus

$$P(f) = 2 \int_0^{\infty} W(p) \cos 2\pi fp dp$$

Dans le cas de notre série discontinue d'échantillons, on peut écrire, selon Tukey, une première approximation de $P(f)$

$$L_q = W_0 + 2 \sum_{p=1}^M W_p \cos \frac{pq\pi}{M}$$

dans laquelle L_q représente les contributions des fréquences fondamentales et harmoniques successives pour $p = 1, 2, \dots, M$.

SYSTEMS OF ECHOLOCATION

by

Thomas C. POULTER

Background

In 1793 the brilliant scientist Lazzaro Spallanzani¹ observed that a captive owl became quite helpless when the candle which lighted a room was blown out, but that a bat would continue to fly about the room with no apparent loss of its ability to avoid obstacles. These observations started Spallanzani on a series of experiments which demonstrated that blinded bats could avoid obstacles just as well as bats with normal vision. At about the same time L. Jurine¹ was conducting experiments, later confirmed by Spallanzani, which established the role of the ears in flight navigation by blinded bats.

Thus Spallanzani and Jurine knew more about this phenomenon than was to be learned by scientists for the next 140 years¹. Because their results were rejected and ridiculed by the most influential philosophers and biologists of the time, their only finding to be preserved in natural history publications of the 19th century was the fact that blinded bats fly normally.

But as higher speeds in travel became facts of modern life, and after such disasters as the sinking of the Titanic in 1912, man began to feel the need for a nonvisual means of detecting objects at a distance. By this time, also, a better understanding of sound frequencies above the audible range was developing. As early as World War I the Navy began to develop

listening devices for use on ships to detect the presence and direction of other ships. From these comparatively crude beginnings both sonar and radar evolved during World War II.

Parallel to the development of man's engineered devices has been re-awakened interest in forms of biological sonar. Donald R. Griffin,¹ as an undergraduate at Harvard, was familiar with the view that bats felt with their wings, but was unaware of the work of Spallanzani and Jurine. Griffin enlisted the cooperation of Prof. G. W. Pierce¹, who had developed some new techniques for studying sounds containing frequencies above the audible range, and in 1939, Robert Galambos¹ joined Griffin in the investigation of echolocation by bats, thereby laying the foundation for the now rapidly expanding fields of bioacoustics and biosonar. Dr. Griffin's book, *Listening in the Dark*,¹ is the most complete treatise on biosonar in current literature, and his research on bats has been the basis for much of the work today.

Increasingly strong evidence is continually accumulating that many species make use of their own noise as they fly, swim, or travel on foot as a source of sound for echolocation as postulated by Spallanzani for the bat more than 160 years ago. This author established in 1963 that penguins use some form of echolocation for retrieving fish in the dark although it has not yet been possible to isolate signals from the water noise produced by their swimming, and blind subjects find that any traveling aid which involves their wearing headphones deprives them of more general information about their surroundings than is contributed in new information.

Many laboratories throughout the world are making extensive studies of bioacoustical sounds from the oceans. Marie Poland Fish and her staff

at the Narragansett Marine Laboratory² have recorded underwater signals of 400 species of fish (from about 100 known families), 25 species of cetacea, and 10 species of pinnipeds. And W. E. Schevill, at Woods Hole Institution of Oceanography,³ has recorded signals of many of the cetacea and other marine mammals.

Man, that favorite among mammals, also has echolocation abilities that are currently receiving much study. Only recently have quantitative measurements of man's echolocation capabilities been attempted. In 1962, Winthrop N. Kellogg⁴ found that two blind subjects could make size discriminations, sense changes in an object's perceived size with changes in distance, and discriminate between a target covered with denim and one covered with velvet. In more recent experiments, Charles E. Rice has studied five blind subjects, using echo information produced by their own differing types of vocalizations, to determine the minimum size target they could detect. The vocalizations included such sounds as short or continuous whistles and hisses, pronouncing words with "f" or "s" sounds, and sharp tongue clicks. All subjects could detect targets as small as 4.5 cm in diameter at a distance of 60 cm and could detect a 25-cm-diameter target at a distance of 2.7 m. In other tests it has been found that these subjects can discriminate among circular disks which differ in area by as little as 10%, at a distance of 90 cm. Some subjects can also distinguish between targets of equal area but of different shapes, such as a circle, a square, and a triangle, at a distance of 90 cm.

Types of Signals Produced by Mammals

As noted above, some of Dr. Rice's¹⁰ blind human subjects used sharp tongue clicks in their echolocation tasks. In the case of very short-

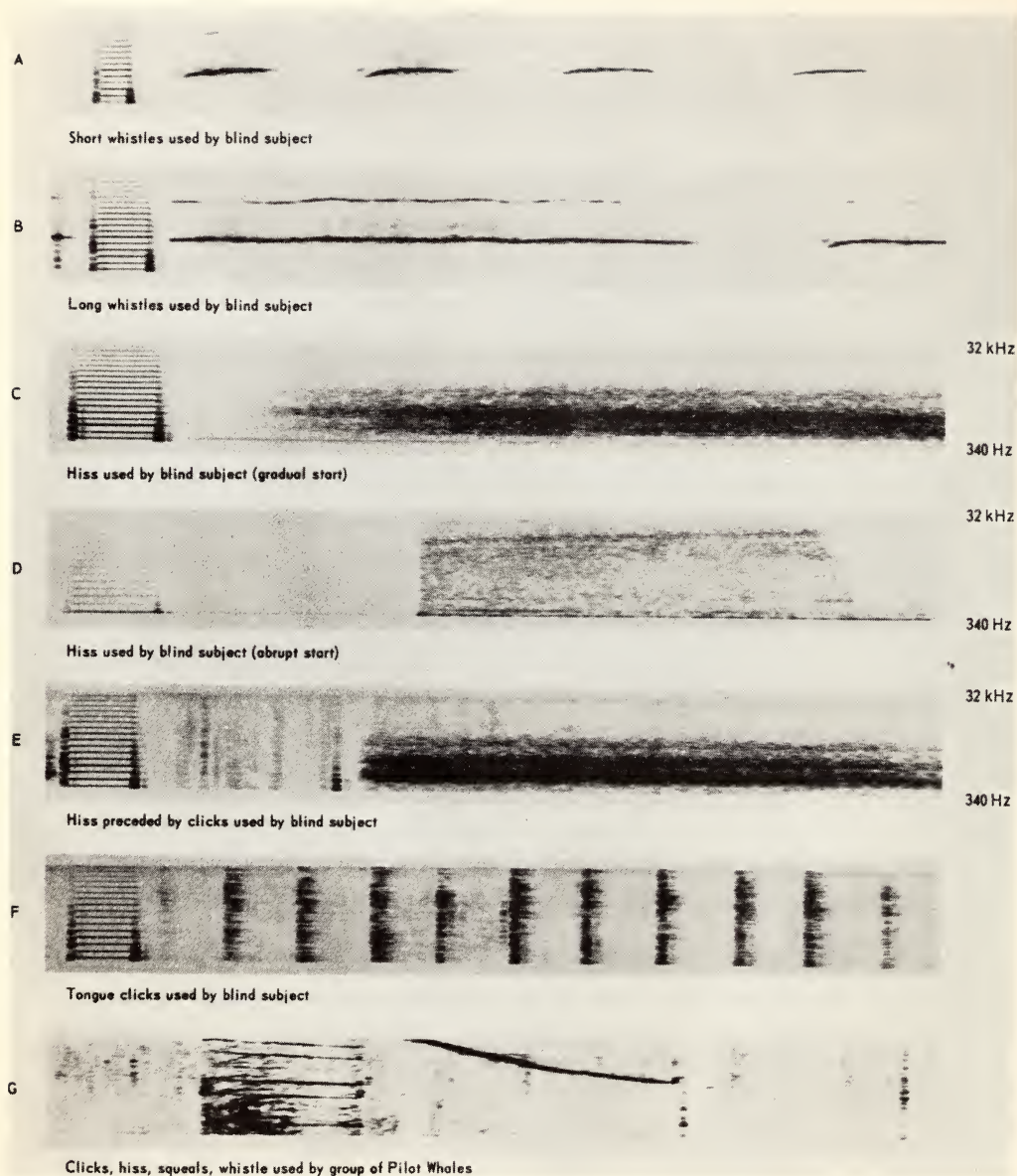


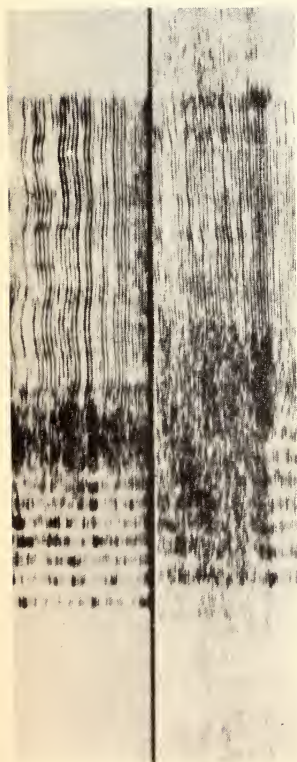
Fig. 1

duration clicks, the echo is more apt to be isolated by time from the initial signal; one would therefore surmise these clicks should be more efficient for echolocation than, say, the continuous hiss. However, blind persons using a constant hiss sound perform equally well, since they perceive the echoes from a target as minute sound fluctuations. It is therefore clear that more than one type of signal can be used successfully in echo-ranging.

Figure 1 shows sonagrams of different types of signals used by blind human subjects to detect the presence of a target and to make size and shape discriminations. The signals were whistles, hisses, hisses preceded by and containing throughout a series of clicks, and tongue clicks. Also in Fig. 1 is a sonagram of a pilot whale, Globicephala melaena, which contains a combination of all the types of signals contained in the sonagrams from blind human subjects, plus a cry superimposed on a hiss and a large sweep in the frequency of the whistle.

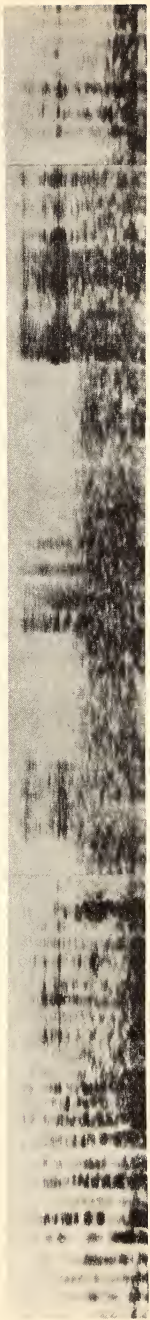
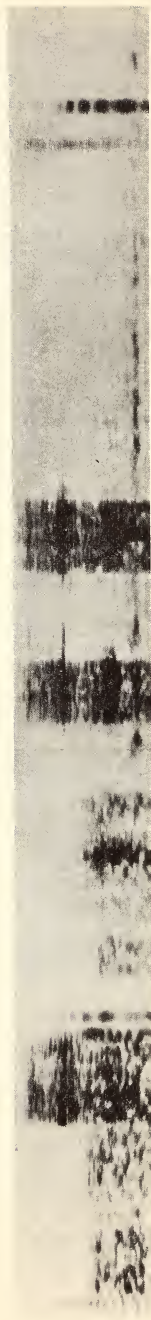
That many organisms such as bats and certain birds, cetacea, seals, and sea lions use an active sonar to locate food prey and to avoid obstacles has been well established.^{1, 3, 4, 6} While they seem to prefer sharp clicks for this purpose, in the light of the sonagrams in Fig. 1 and recordings made in their natural habitat we certainly cannot rule out the possibility that most of their other signals are also being used in their echolocation activities.

There is no sure way of determining just by listening to a signal whether it is an active sonar signal or merely a general bioacoustic signal. Underwater signals are arbitrarily divided into echo-ranging (sharp clicks which could, in man's opinion, be used for this purpose) and communication signals. However, the fact that blind people can use such a wide range of



KILLER WHALE SIGNALS PRECEDED BY CLICKS

Fig. 2



BLUE WHALE CLICKS AND SIGNALS FORMED BY GROUPING CLICKS

Fig. 3

active sonar signals makes it clear that division of bioacoustical sounds into echo-ranging and communication signals on the basis of presence or absence of "clicks" is not justified, however convenient it may be for purposes of reference.

Indications that some species, at least, may use any of their vocalization signals for long range echolocation are found in recordings of the signals of the killer whale. In open water where the whale may be interested primarily in boundary conditions, or if confined in a limited area by a barrier through which the whale can echo-range, it will most likely use the signals it normally employs for communication. On the other hand, in a small enclosure or in a narrow channel such as an open lead in polar ice, the killer whale will use a series of sharp clicks almost exclusively. In the comparatively wide channels and bays of the Pacific Northwest portion of the United States the recordings of the signals of the killer whale frequently contain echoes from much of their vocalization. It is, however, most uncommon for a killer whale to use predominantly clicking signals under these conditions. This is amply illustrated in some recordings made of Namu⁹ in his winter quarters in Rich Cove with echoes from rock ledges at a distance of one-half mile across Rich Channel. Likewise, recordings made of a group of 12 or 15 killer whales in a narrow open channel in McMurdo Sound in the Antarctic contain clicks almost exclusively, with only an occasional "communication" type of signal.

For many animals which have been thought not to produce echolocation clicks, a more careful examination shows that many of their signals start with a series of clicks so closely associated with the signal that our ear does not resolve them. In other species, including the killer whale, many signals start with a distinct series of clicks, Fig. 2.

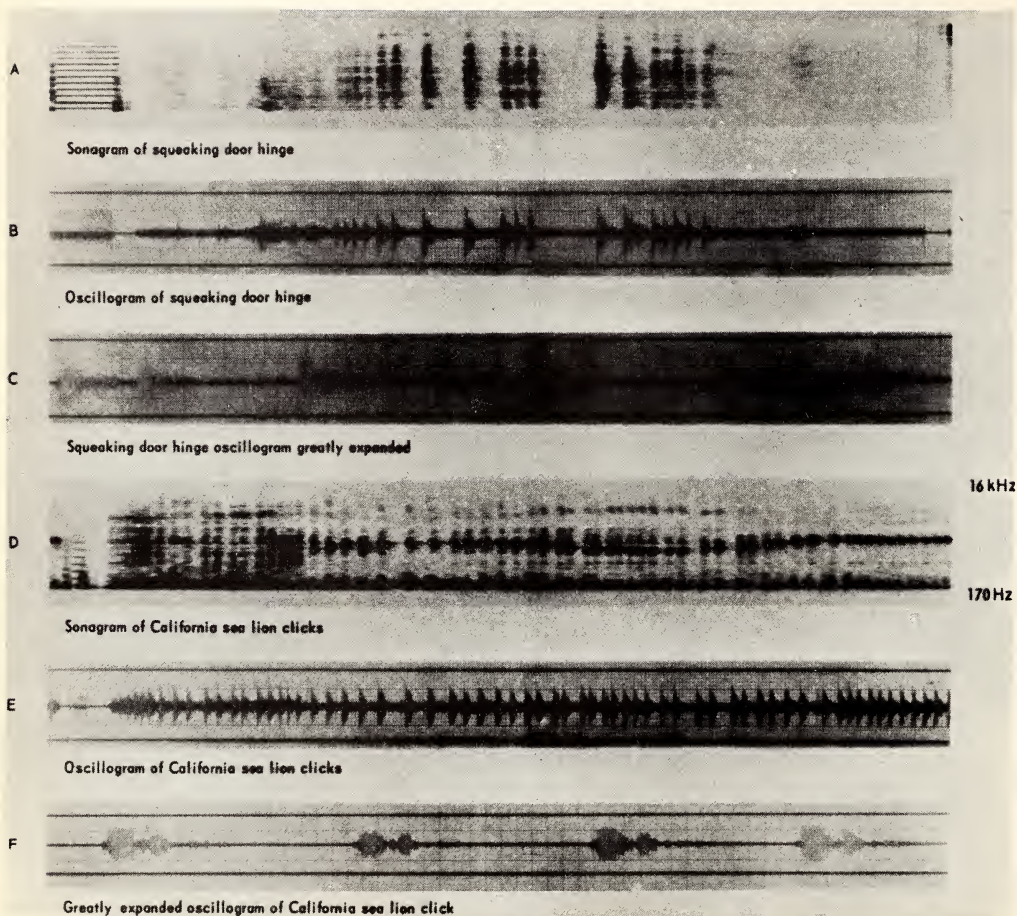


Fig. 4

Until sonagram E of Fig. 1 was made, neither the human blind subject nor those with whom he was working knew that clicks were present and preceded his hiss signal. In contrast, the vocalization of the blue whale, Fig. 3, consists almost exclusively of clicks and his communication type signals are formed merely by spacing the clicks so close together in groups that our ear does not resolve them.

Clicks whose basic frequency may vary from less than 1,000 Hz to in excess of 100 kHz may have a very high repetition rate. Whether it is called a clicking rate or a signal frequency becomes a matter of semantics, for a clicking rate of even isolated clicks is just as truly a portion of the frequency of the over-all signal as are the frequencies within the individual clicks.

Some of the more common underwater signals of marine mammals are squeals, whistles, moans, grunts, chirps, barks, and clicks. If clicking sounds are emitted at a high rate they are described variously as "rusty gate," "creaking door," signals. Figure 4 shows a sonagram and two oscillograms of an actual squeaking door hinge, compared with a sonagram and two oscillograms of the "squeaking hinge" signal of the California sea lion. Note that only by expanding the time scale can the sea lion's signal be distinguished from the actual squeaking door hinge. These pulses may rise to full intensity within the first few cycles, or indeed within the first half-cycle, and then drop off gradually to zero amplitude, or they may go through one or more minima, causing a double, or multiple-pulse, effect.

Signal Frequencies

In both sonar and radar, the trend today is to obtain more information about the target from returning echoes--an area in which biological



BULL BARK



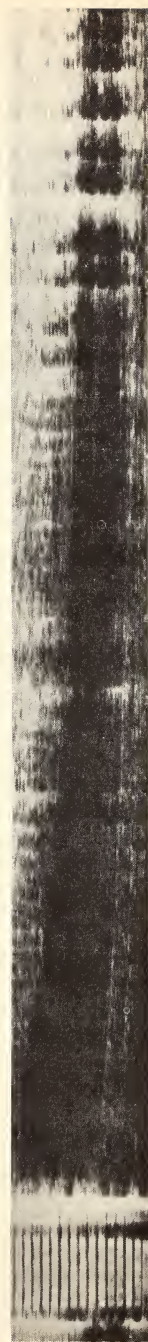
BULL ROAR



BULL BARKING



BANG



BANG

WHINNY

SWEEP FREQUENCY CLICKS

Fig. 5

organisms are far ahead of man's feeble efforts. The frequency required for purposes of echolocation is a function of the size and nature of the target and the type of information desired. In general, the wavelength of the signal should not be greater than twice the dimensions of the target, in order to produce a fair echo; thus for the same size of target, the frequency of the signal in water must be about five times as high as in air.

Dr. Griffin¹ has shown that some bats use frequencies as high as 260 kHz for a wavelength of 1.27 mm, or a target size of less than 1 mm.

Dr. Norris¹¹ recently confirmed frequencies of 270 kHz for Tursiops, for a wavelength of 5.7 mm, which would correspond to a target size of about 3 mm; he has found that blindfolded porpoise will indeed pick up objects in that order of magnitude from a smooth-bottom tank.

Even though the underwater clicks of the marine mammals contain some very high frequencies, the major portion of the energy is usually below 20 kHz. Underwater barking and bangs of the California sea lion produce very similar sonagrams, see Fig. 5, but actually sound entirely different from each other. In the bang, all frequencies start at the same time and rise rapidly to a high level, thus causing a sudden rise in energy, but in barking the higher frequencies have a delayed start and the rate of increase in intensity is lower.

Auditory Reflex

Any attempts to compare very short-duration animal signals such as clicks only by listening to them can be grossly misleading. The rate of onset of a signal may so affect the protective auditory reflex in our ears, and the recovery time may be so slow, that we hear only the onset of the signal. Thus two click series which are very similar except for the initial

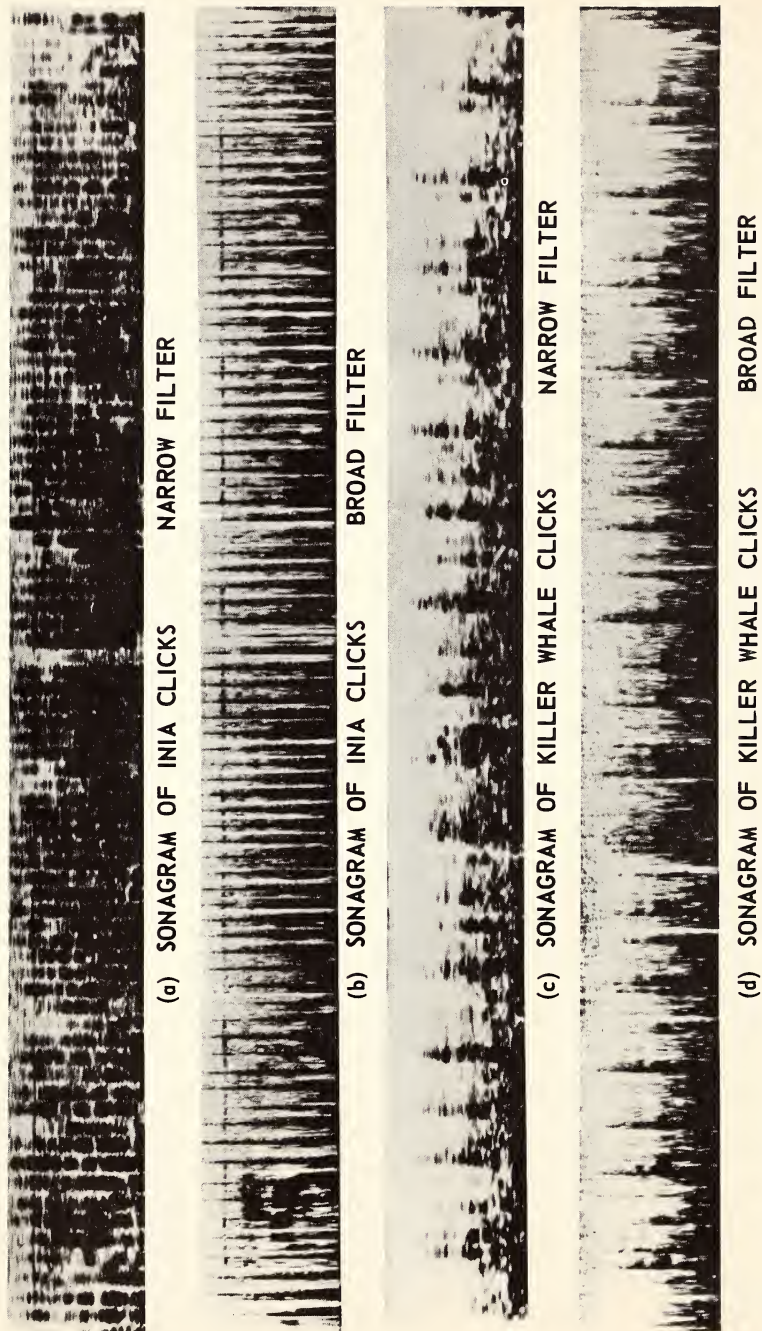


Fig. 6

rise time may sound entirely different. If a tape loop of a series of clicks in which only alternate clicks have a very steep rise time is played in one direction, the alternate clicks sound entirely different from the intervening ones; if the tape is played in the other direction, all the clicks may sound identical. How loud clicks sound is also greatly affected by the rise time of the signal.

In Fig. 6 the two top sonagrams of clicks produced by Inia, there is less background noise and the sonagrams stand out more distinctly than do those for the killer whale in the last two sonagrams. However, because the killer whale sonagrams represent clicks which have very sharp rise times, they sound much louder and more distinct than do those from Inia. It is interesting to note here that the military take advantage of this effect in firing large guns when personnel must be close to the gun--for example, in a tank. The tank crew must wear headphones for communication purposes; just before the gun is fired (electrically), a loud pulse is introduced into the headphones. When the auditory reflex has densensitized the ear, the gun is fired and the blast is not painful.

Sweep Frequency

During World War II the Navy developed what was considered a completely new concept of a sweep frequency signal for echolocation; this technique produced a better echo for target identification purposes. We have since found that for millions of years this method has been used by several species of pinnipeds and cetaceans--the Weddell seal and leopard seal in the Antarctic, the bearded seal and bowhead whale in the Arctic,⁸ and the killer whale.⁹



STELLER BULL THREATENING GROWL



STELLER BULL SNORT



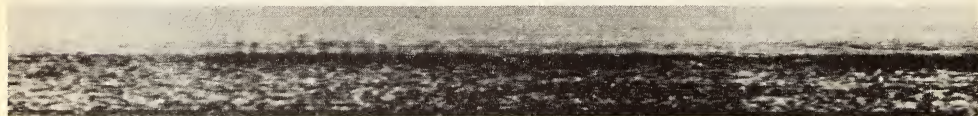
STELLER BULL SCOLDING CALL



STELLER BULL UNDER WATER SIGNAL



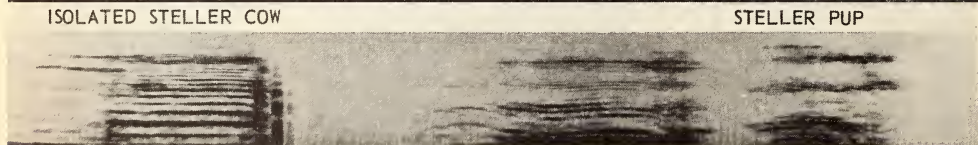
STELLER BULL UNDER WATER CLICKS



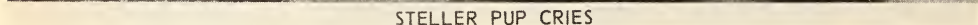
STELLER COW WITH ROOKERY BACKGROUND



ISOLATED STELLER COW



STELLER PUP



STELLER PUP CRIES

Fig. 7

For long range, large target echolocation, the sweep frequency method produces a more distinct echo, as shown by magnetic tape recordings of echoes from a rock ledge half a mile from the signaling killer whale. Also, use of a sweep frequency permits determining range, by comparing or "beating" the frequency of the echo against the frequency of the outgoing signal at the time the echo returns. It has been shown that the bat may shut off its hearing while sending out its signal, and considerable evidence is accumulating that this same phenomenon occurs in other species, including some of the marine mammals. This auditory reflex prevents desensitizing the hearing of the organism just at the time that it is listening for the very weak echo and hence needs its maximum sensitivity.

Echo-Ranging Purposes

Animals of many species use echo-ranging techniques in a variety of ways, for a variety of purposes. For example, many species can discriminate not only size, but also texture, of a target. Although no minimum size discrimination has been determined for the California sea lion, the author⁶ has established that they can make texture discriminations, in total darkness, between pieces of horse meat and fish of the same size. Correspondingly, Dr. Griffin¹ has shown that bats can discriminate between meal worms and plastic pellets tossed into the air in total darkness.

In the case of baleen whales, as contrasted with toothed whales, echolocation signals must meet entirely different sets of specifications. Since the food of the baleen whale is large masses of widely dispersed, small-sized krill and other plankton, this animal uses a different sonar signal from that of the toothed whale when it is seeking out a single, much larger organism.

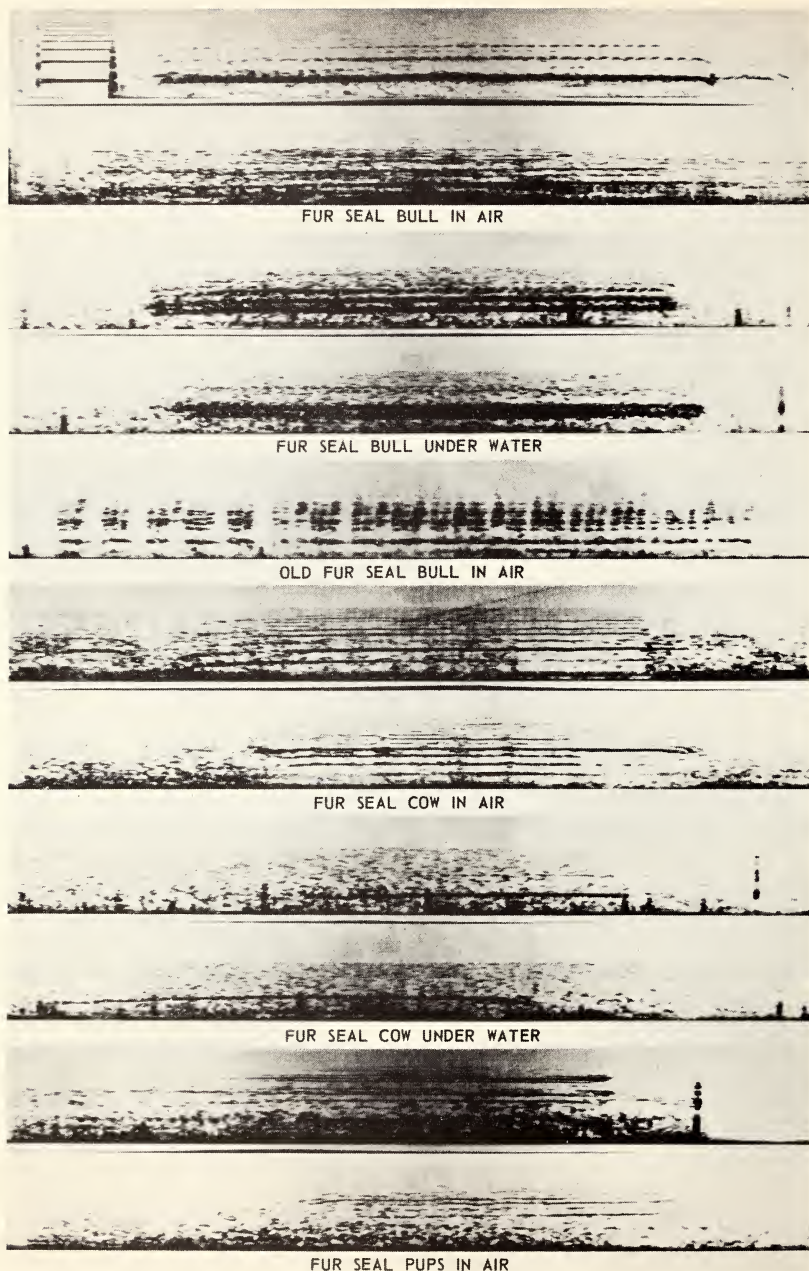


Fig. 8

It has also been observed that blind sea lions use a crude short-range sonar out of water. These animals have been seen to follow an irregular rock wall, keeping from 60 to 100 cm from the wall and progressing only when barking, with their heads turned toward the wall most of the time. When approached by a human being, a blind sea lion would change the tempo of its barking and usually move away toward the water. When it was not barking, the animal could be approached from downwind close enough to touch it. If touched with a stick from a distance of about 3 m, the sea lion would usually bark a few times and move several feet away. If touched from a distance of only 60 to 100 cm, it would move directly away from the observer and then angle toward the water, barking as it went.

More and more new species are being added to the list of organisms which use some form of echolocation so that at the present time it covers the range from small insects to the largest living mammals.

Although no recordings have been made to date of the underwater vocalization of the hippopotamus, Dr. W. M. Longhurst¹² finds that they use either a passive or an active sonar, or both; as a result they can avoid obstacles even while charging a small boat from a distance of a few hundred yards without surfacing and through such muddy water that visibility could not be as much as 30 cm. Their progress in the shallow river water could be followed by the wake produced on the surface of the water.

As in the case of the bats, where the particular technique employed in echolocation varies from one species to another from a very elaborate system to not using sonar at all, so it is with the pinnipeds and cetaceans. There are cases (for example, among Zalophus and Tursiops) where a



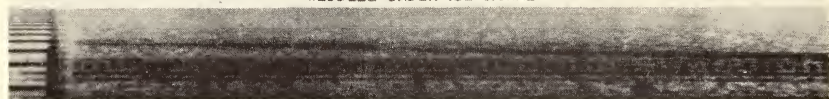
WEDDELL SEAL COW CHIRPING



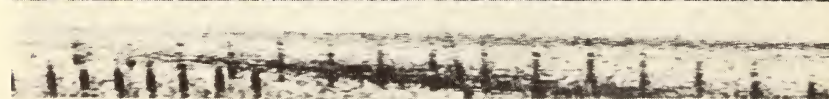
WEDDELL SEAL BULL CHIRPING



WEDDELL UNDER ICE SIGNAL



WEDDELL UNDER ICE SIGNAL



LONG CONTINUOUS WEDDELL UNDER ICE SIGNAL

Fig. 9

pinniped and a cetacean may use echolocation signals more nearly alike than those of two animals of the same order. Some species, such as the Steller sea lion and the fur seal, apparently use their normal in-air vocalization for underwater echolocation signals, see Figs. 7 and 8.

The Weddell seal and the bearded seal both repeat a long series of underwater signals, sometimes extending over a period of as long as 30 seconds for the Weddell seal and one minute for the bearded seal. In both cases they start at a high frequency of a few thousand cycles and a repetition rate as high as 200 pulses per second and sweep down in both frequency and repetition rate to under 100 Hz and a repetition rate of less than one per second. The bearded seal covers a somewhat broader frequency range and pulsing rate than does the Weddell.

The successive pulses, however, differ widely in the two species. In the case of the Weddell seal these pulses consist of a discontinuous succession of what resembles a modulated sine wave, Figs. 9 and 10. On the other hand, the single pulse of the bearded seal consists of a descending frequency of more nearly constant amplitude. The next pulse in the series then starts at a slightly lower frequency and again sweeps down over about the same range, so that the sonagram has a sawtooth form, Fig. 11.

The leopard seal in general has a continuous series of pulses with a low or a high frequency; occasionally the signal sweeps from the low to the high frequency series. When this occurs, as the frequency sweeps up the repetition rate goes up correspondingly. Another common procedure of the leopard seal is to use a very high repetition rate for about one-third second and then, while maintaining the same basic frequency, suddenly

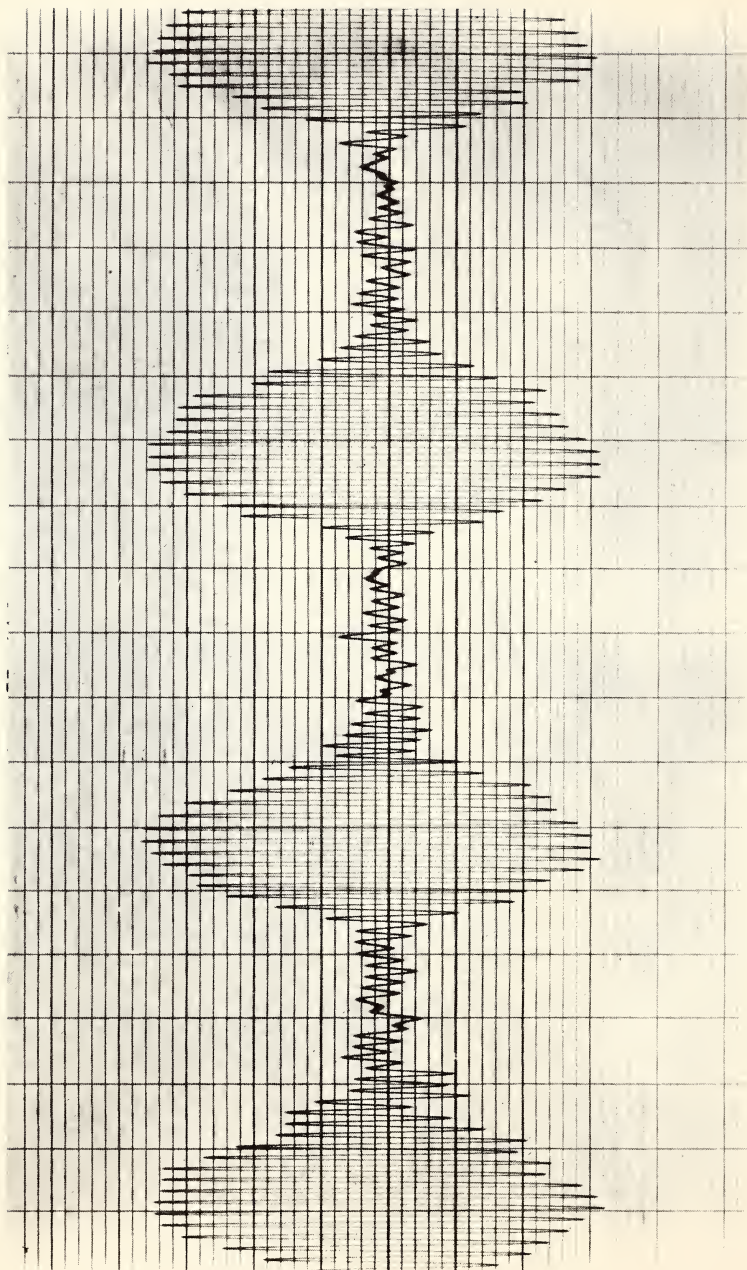


Fig. 10 Oscillogram of Weddell Seal under Ice Signal

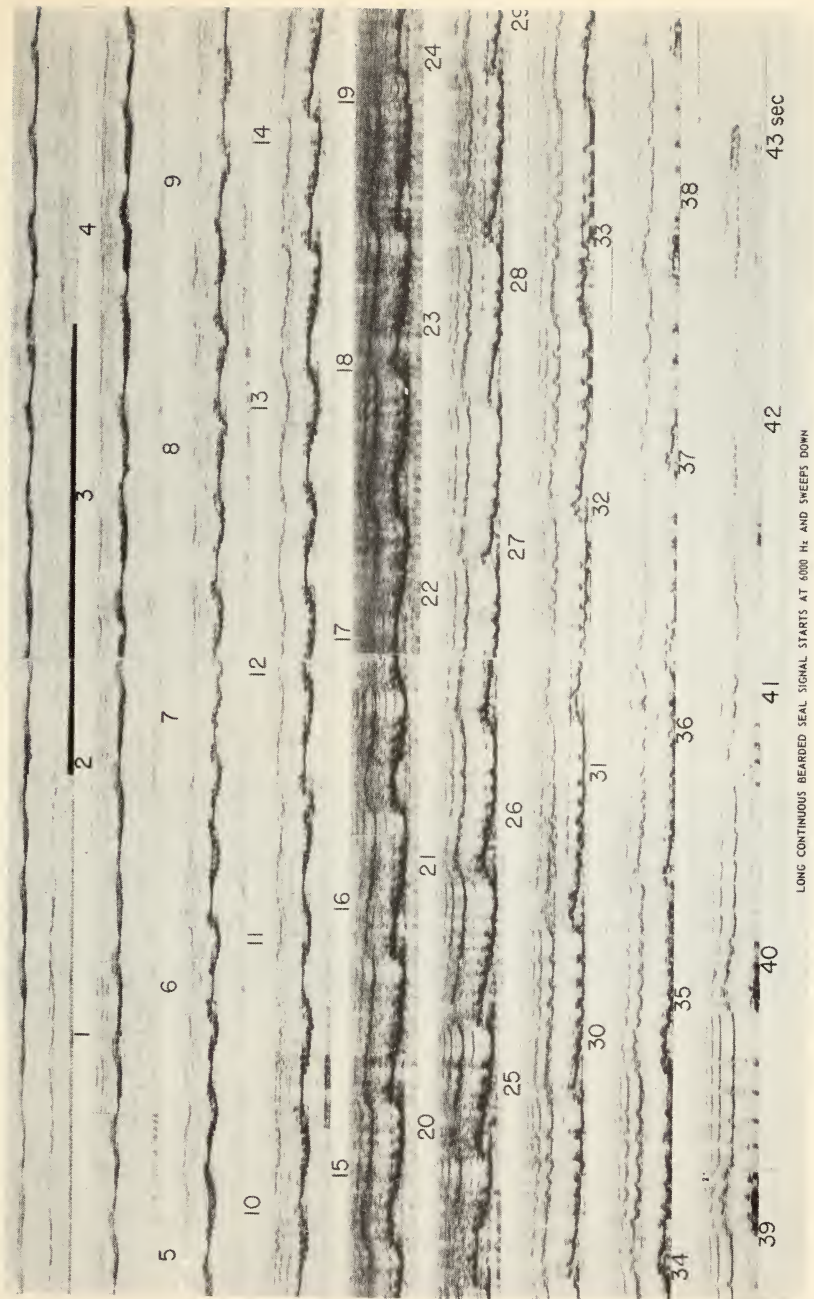
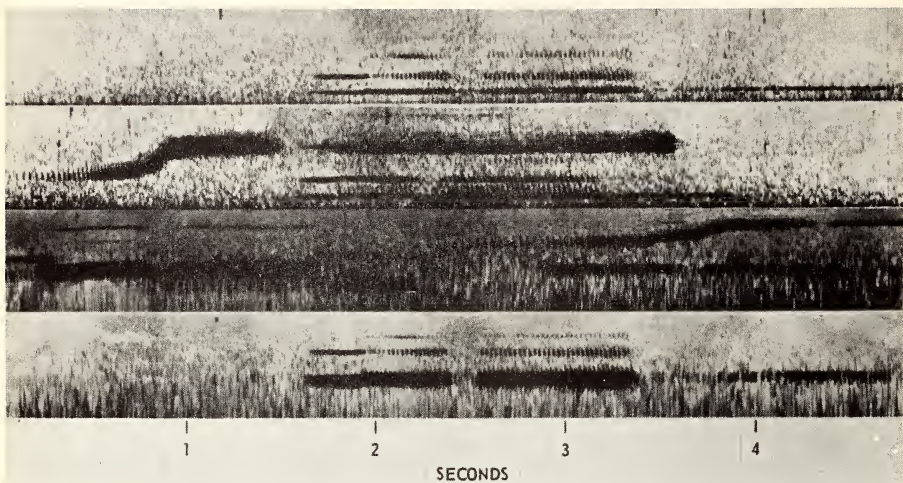
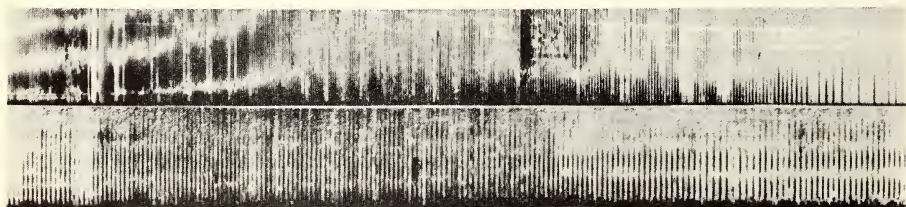


Fig. 11 Long Continuous Bearded Seal Signal Starts at 6000 Hz and Sweeps Down to 200 Hz



TYPICAL HIGH AND LOW FREQUENCY LEOPARD SEAL SIGNAL WITH UPSWEEP FROM LOW TO HIGH. Linear scale 40 to 4000 Hz. Since Penguins use underwater sonar they may be responsible for some of these signals.

Fig. 12



INIA CLICKS

Fig. 13

to shift to a lower and slowly decreasing repetition rate for about a half-second, following which the signal is discontinued for some seven-tenths of a second and then is continued at the same frequency and at about the same repetition rate for another one or two seconds, Figs. 12 and 13.

For its underwater signals, the Amazon dolphin, Inia, uses a long, continuous series of very fast clicking rate of narrow, clearly defined clicks. The humpback whales are the biggest showoffs and the noisiest and best performers for the bioacoustician. As long as there is more than one whale in the general vicinity, there will be much vocalization, with both echolocation and communication signals. The bowhead whale of the Arctic has a distinctive loud moan which may be an ascending or descending frequency signal. It usually consists of a narrow frequency range, continuous signal accompanied by a slightly higher frequency, rapidly pulsed signal, or the continuous signal may be pulsed somewhat similar to that of the bearded seal but confined to a somewhat narrower frequency range, Fig. 14.

At Stanford Research Institute we are attempting to develop computer techniques to replace some of the more laborious and time-consuming analytical methods for studying the signals of marine mammals. One of these programs is working primarily on analyzing the signals of the killer whale. The original direct recording of the animal is programmed through an analog-to-digital conversion with the tape running at actual or a reduced speed. The computer picks digital values for the amplitude of the signal at the rate of 144,000 points per second and records these data on a second,

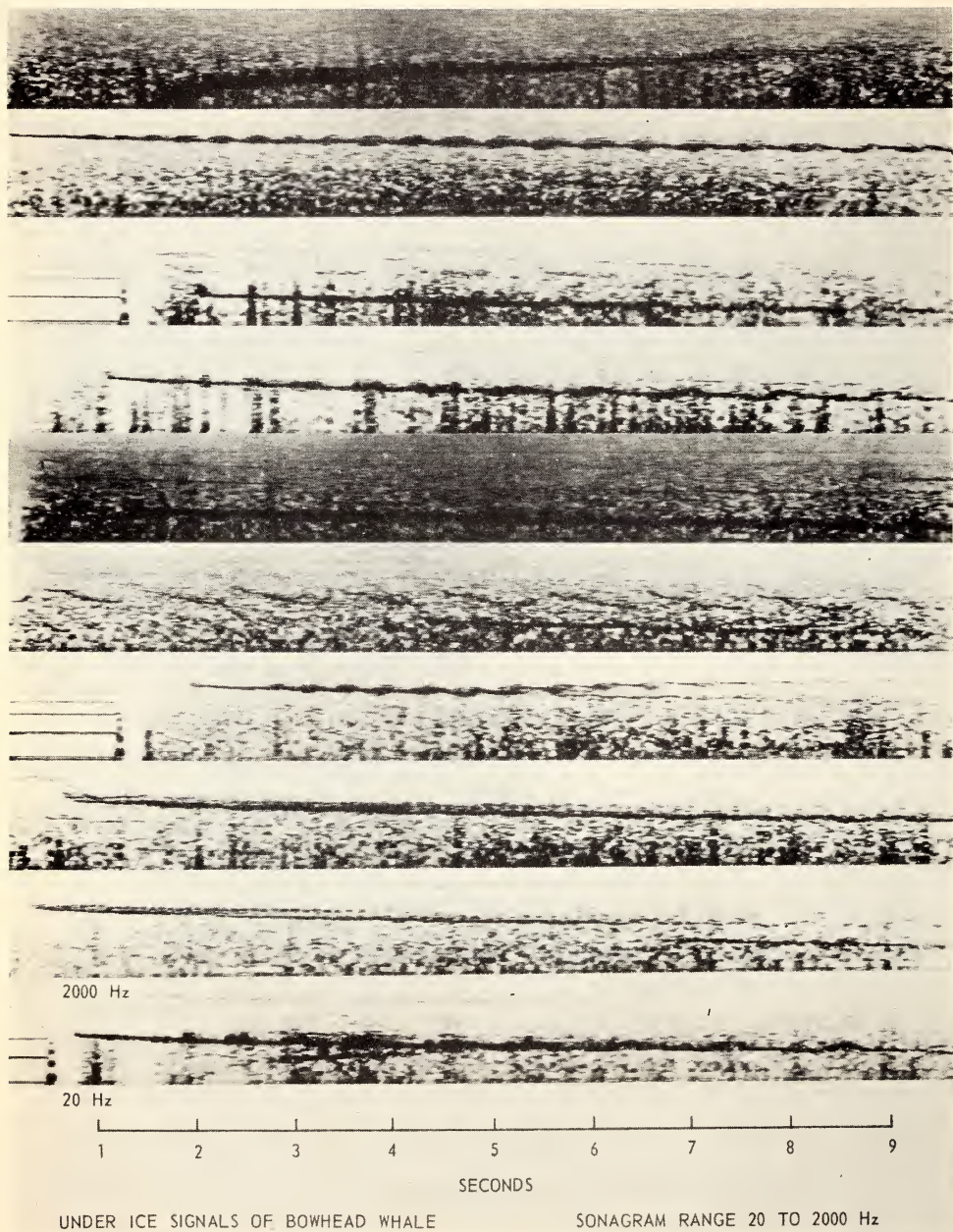
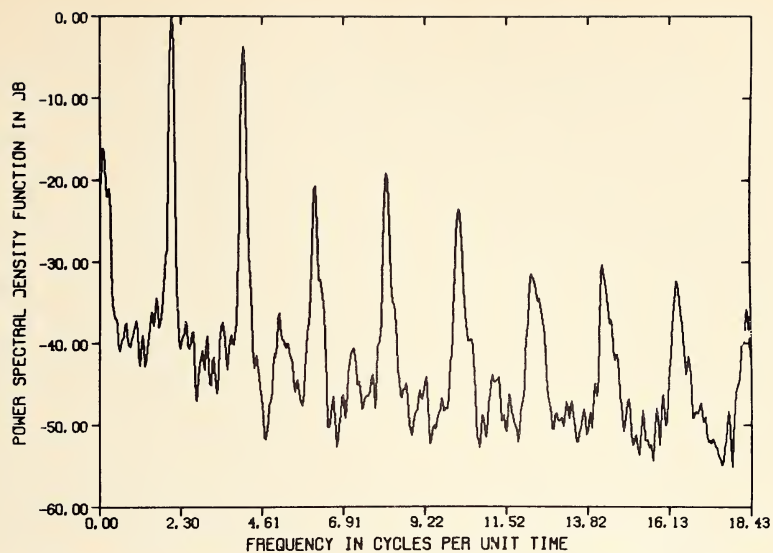


Fig. 14



KILLER WHALE SIGNAL- PSD FUNCTION IN DB, SECOND SMOOTHING

Fig. 15

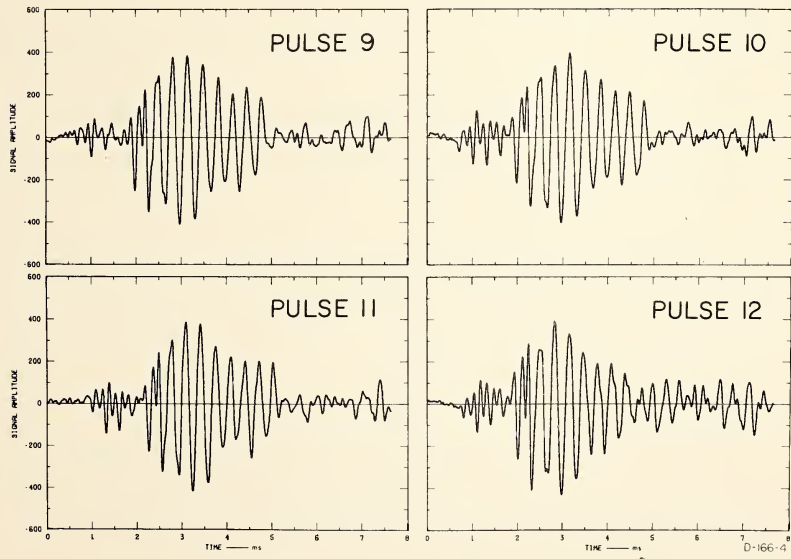


Fig. 16

or digitized, tape. In this manner the points are picked close enough together that the wave form of the original signal can be accurately reproduced at any desired scale. In the case of the killer whale signals, a mass spectral density analysis is being made by using the digitized tape as input into the large digital computer which is programmed to determine the number and intensity of all of the harmonics at any instant in time and to determine the phase relation of each of those harmonics, if desired, Fig. 15.

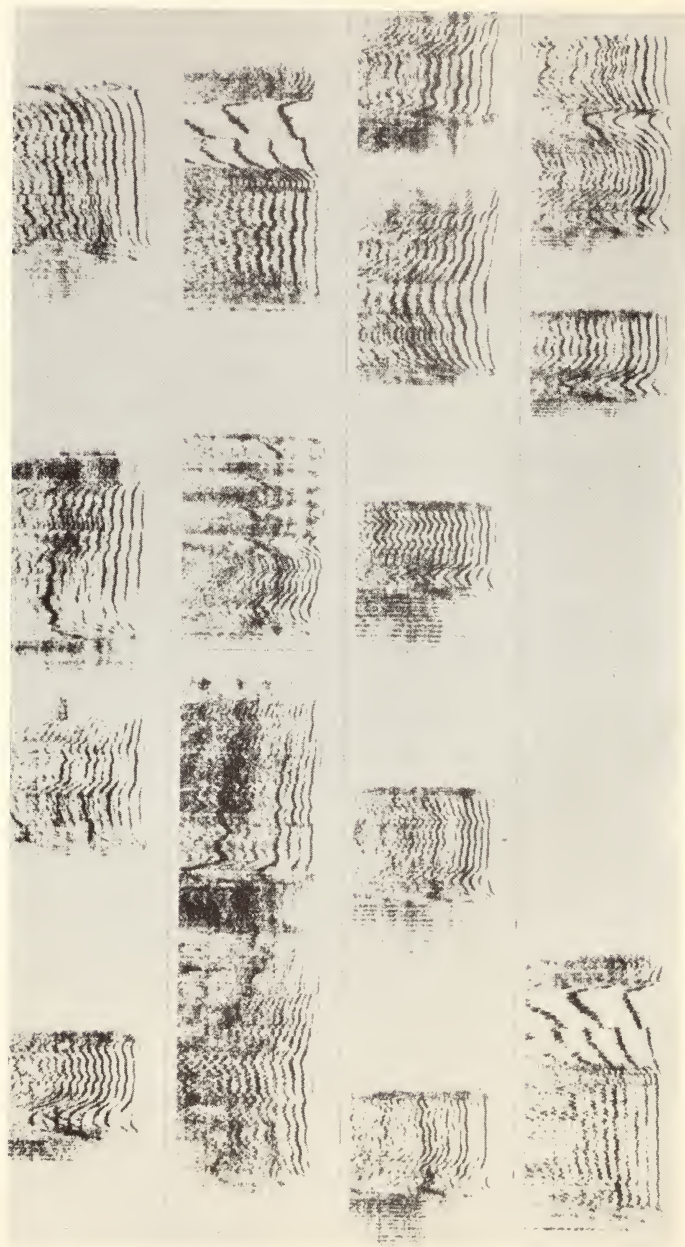
Attention was first called to the double pulse by the author in 1963 for the California sea lion and later confirmed for Tursiops by Dr. Norris.¹¹ Reference to this phenomenon can be readily observed throughout the literature in published oscillograms of the signals of a great variety of species. The second computer analysis program being undertaken at Stanford Research Institute is using the double-pulse signal of the California sea lion in the development of a computer technique for the evaluation of bioacoustic signals for purposes of echolocation.

This program should provide an answer to the manner in which the double pulse is used, the maximum and minimum ranges for which the signal is suited, its accuracy at different ranges and range rates, and minimum size of target the animal can detect. It should further yield valuable information concerning the mechanism for these animals' discriminatory capabilities. Work thus far indicates that, for short ranges at least, the range is determined by the phase relation between the echo and the following pulse; since the echo can be separated from the following pulse and its frequency characteristics can be compared with the precursor pulse, we believe it may be possible to determine a mechanism to account for their discriminatory ability, Fig. 16.

In the third, and more general computer program we are trying to speed up the present time-consuming Sonagraph and oscillograph techniques. The Sonagrams are run off on 35 mm paper while the original magnetic tape recording is being run at recording speed. Figure 17 shows Sonagrams of the killer whale's signals made by this technique. It is therefore possible to prepare in one day the Sonagrams on 35 mm paper of as much tape as would require 20 man-years using conventional Sonagraph methods. At the rate that pattern recognition techniques are now being developed, the analysis of bioacoustic data computer techniques should advance our knowledge of bioacoustics at a greatly accelerated rate.

ACKNOWLEDGEMENTS

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SONAGRAMS OF KILLER WHALE SIGNALS

Fig. 17

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Abstract

The recognition that facial vision was echolocation, and the discovery that most marine and many terrestrial mammals have some echolocation capability has led to an ever expanding participation in this field by the scientists of the world.

Sonar signals may vary from such noises as the species make as it travels by whatever means to the most sophisticated, directional, frequency modulated system found in some bats. The entire range of vocalization of many species may be used for either echolocation or communication. Every important advance in man's radar has later been found to exist in some animal's sonar. Their signals are not only species specific, but in many cases sex specific, such as the killer whale, fur seal, elephant seal, Steller sea lion and many others. Even so, different species may have very similar systems such as the Antarctic Weddell, and the Arctic bearded seals or the clicks of the California sea lion and the porpoise.

Stanford Research Institute has developed computer techniques for producing continuous sonagrams at the recording speed; and with the development of pattern recognition, signal analysis should be speeded up by orders of magnitude.

FACIAL VISION REHABILITATED

by

Ivo KOHLER

Among blind human beings there are many (particularly among those who are well-experienced and are able to move about alone) who seem to depend not on their ears, but upon certain skin sensations for the purpose of detecting obstacles. They describe these skin sensations, which mostly occur within the domain of the temples, the forehead, and the cheeks, and sometimes up to the shoulders, as being "similar" to a slight touch or pressure. They continue to say so although everyone of them can easily be convinced of the pure auditory origin of the sensation in question, i.e. it disappears completely when hearing is eliminated.

So, it was first of all our purpose to clarify the meaning of that puzzling kind of sensation often called "facial vision". Unfortunately, there are no words in any language by means of which this quality may be described precisely.

One group, for example, reports the sensations as similar to coming into contact with a cobweb upon one's forehead, others compare it with a fine veil thrown over one's head, and often it is referred to as being something in the nature of a nightmare.

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Fig. 1

"Facial Vision"

Most frequently reported sensitive areas of "facial vision".

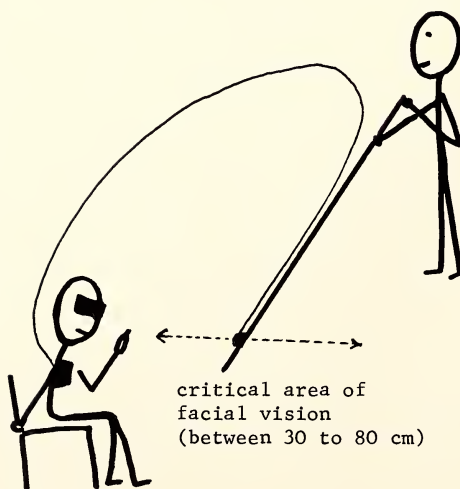


Fig. 2 (for explanation see text)

However, as soon as stimuli such as a fine veil were actually used for stimulation, every blind or blindfolded subject of our group was immediately able to assert the sensations produced in this manner were really not of the same nature as facial vision. If, for example, blind persons were induced to come into real contact with very thin threads or hair, if electrically charged ebonite rods were moved towards the subjects' faces, or infrared radiation used, etc., these in no case, evoked the typical skin sensations which occurred in the presence of obstacle surfaces. The conclusion of all this could be that the phenomenon in question has to be characterized by a quality of perception of its own, which, if at all, must be caused by more complex stimulus situations acting upon the skin than those used by us. In order to clarify the situation from the outset, we carried out a most crucial experiment. Continuing some of the famous earlier work of DALLENBACH and his group, we paralyzed the skin areas in question.

In all cases the result was startling. In spite of complete anaesthetization of critical areas on the skin, normal facial sensations continued to be reported.

We had one special group of skin users (the facial-vision type of our blind and blindfolded subjects) whose skin was anaesthetized on the right half of the face only. These subjects were then sent along a corridor, and were told to walk in the middle until they reached the end. As a result of paralyzing one half of the face, the corresponding facial sensations on

that half should have been obliterated, thus causing the subjects to markedly drift away from the middle line of the corridor off to the side corresponding to the paralyzed side of the face.

This effect however, failed to occur in all cases investigated; we used a total of 13 subjects (blind and blindfolded) who followed the procedure described.

In addition to this result there was another, for which we are indebted to the fact that at the time of these tests some cases of neuralgia happened to be treated at our Innsbruck clinic. We obtained permission to carry out obstacle tests with these patients before and after they underwent operations to block off the trigeminal nerve by injection of alcohol into the ganglion Gasserii. In those cases where we were able to cause facial vision before the operation, we found that it was retained after the operation had been performed. According to some of the patients, "facial vision" was even more intense than before the operation because the superimposing sensations of pain felt previously were now lacking. The subjects in this case were sighted and blindfolded only during our experimentation.

On the basis of these results it may be taken as certain that the facial sensations in question are at least a central nervous process and have nothing to do with any kind of skin receptors.

It would simplify matters greatly if it were possible to prove the existence of direct nervous connections between the acoustic center and that center in the brain which is responsible

for touch and pressure on the face and adjacent areas of the skin. In the case of human beings this must, however, be denied from an anatomical point of view.

The nearest approach to the problem in question was made by v. BEKESY (1936). Very intense deep sounds which are near the auditory threshold cause distinctly noticeable skin sensations in the auditory passage and within range of the outer ear. The sensations, as v. BEKESY was able to prove, can not be explained by the direct effect exercised by sound waves upon the skin. However, this result also cannot simply be applied in the case of facial vision. In the case of facial vision the sound intensities involved are usually much lower; furthermore, comparatively stronger high frequencies are mixed together, and finally, the area of the skin involved is considerably larger. Only the following result of our own investigations is interesting in connection with the result obtained by v. BEKESY: If a subject is offered the choice of sounds of different pitches (with great loudness), then he will choose rather low frequencies (from 20 to 90 c) appearing as "approximately similar" to the facial sensations in question. Very high and loud sounds (of more than 4 kHz) are reported as accompanied by a stinging sensation of pain which, however, is experienced to be "totally different" from the skin sensations near obstacles.

For our purpose we may gather from what has been said so far, that the lower frequencies of a guidance sound and their modifications may probably be more relevant to experienced

facial vision than higher frequencies.

Finally those theories according to which facial vision is a phenomenon based upon suggestion and association do not hold. Such a theory would maintain that the mere fact that a collision with obstacles is expected, would produce a state of alarm in those parts of the body where the collision will happen. Such states of alarm actually exist, and can be aroused at will if, for example, a subject walks about blindfolded in a room, and is informed of the fact that iron rods are distributed in the room at a height corresponding to that of a person's shin-bones. What happens in that case is really that certain peculiar sensations are reported to be experienced on the shin-bones but these sensations are of an entirely different nature from facial vision sensations. Even if a collision with such a rod is strongly expected at the level of a person's forehead, the sensations are by no means comparable with those which are experienced in the case of facial vision. It is a significant fact that the typical sensations of facial vision occur only in the presence and neighbourhood of correspondingly large reflecting surfaces and that, when they occur, they are felt only in the area of the face and occasionally as far down as the shoulders and the chest, but that they are never felt within range of the feet. A phenomenon caused by suggestion should, however, be "projectable" to any part of the body.

If we now discuss other procedures using nothing but sound in order to generate the facial sensations in question, I am anxious to view some of Dr. WILSON's findings from yet another aspect.

The goal was to find the best method for acoustically generating a strong feeling of facial vision without use of real obstacles (i.e. a complete stimulation for the subjects), and we found a peculiar kind of sound modification as being able to do this.

At first, it was noticed that all those persons who had themselves experienced the phenomenon of facial vision in connection with blind orientation, found these sensations intensified as soon as they used a guiding device such as a clicker for their orientation exercises. Furthermore, a few of the hitherto "sound users" converted to "skin users". Finally it was observed that the detection of obstacles and facial sensations did not coincide exactly. From a distance of more than one meter, obstacles are usually acoustically perceptible. On the skin they are perceived from smaller distances (of less than one meter), depending on the size of the obstacle's surface. From these results it is possible to conclude that the conditions causing facial vision are connected with modification of sound taking place in the close vicinity of obstacle surfaces.

Our endeavours to generate facial vision were not promising when we simply modified the amplitude or frequency of a given sound transmitted to the subject by earphones. This was also the case when we used tape recordings taken from life situations of approaches to obstacles. A more useful method in all cases, however, was to construct an undetectable phantom-obstacle consisting of a small sound emitter (an earpiece fixed on a

narrow stick and fed by the signal of the sound guidance device) fixed on the subject's chest. The earpiece re-emitted the same sound as the chest-clicker, and therefore became similar to a real reflecting surface.

To describe the experimental situation in more detail, the subject wearing the guiding device (in this case a clicker) was quietly seated on a chair with instructions to announce the approach of an obstacle as soon as a feeling or sensation was experienced. Instead of an obstacle, however, the above mentioned earpiece was fastened to the rod. From this earpiece the same impulse was emitted (by connecting it parallel with the guiding device) as from the guiding device itself. The rod with the earpiece fastened to its end was in no case detected as an "obstacle" as long as the earpiece was switched off. As soon as it was switched on (so that the guiding device and earpiece emitted synchronous clicks), the strongest facial sensations ever experienced by our subjects occurred within a range of 80 to 30 cm whenever the earpiece was moved towards the subject's face. Outside this range, the "acoustics" of the guiding sound merely appeared to change without the simultaneous occurrence of facial vision. The "critical" range between 80 to 30 cm was equivalent to a real obstacle of about 1 m^2 . None of the subjects (a total of 48 persons) was able to distinguish between a real obstacle and a "pseudo-obstacle" within the critical range, and even after having been informed of the true state of affairs, they continued to be deceived.

It follows that, with this arrangement, a situation seems to have been created, at least within the critical area, in which just those auditory cues were produced which were of importance for obstacle detection, and thus for evoking the experience of facial vision.

Notwithstanding what has been said above, the question still remains unanswered as to why the perceptual response does not remain within the auditory domain but passes over into another modality. On this point I am only able to express a speculative opinion referring to some other perceptual observations: J.J. GIBSON (1950), an authority on perception studies, was able to prove in many cases that very complex stimulus situations within the optical range, (to the extent that they are developed in accordance with strict space-time laws - the so called invariants or "gradients") often find a perceptual correspondence in form of a new and particular quality (or modality). Thus, it may be said, for example, that such highly complicated "transformations" of distances, angles, textures, etc. as are optically generated by moving around, are simply responded to by the perception of selfmovement in a stable world (so-called "visual kinesthesia"). Thus, quite definite arrangements of stimuli and stimuli modifications are responded to, by a peculiar perceptual configuration.

In the case of facial vision we find ourselves faced with an analogous situation, namely, that to a complex acoustic stimulus situation (and only to that situation) there is a

peculiar perceptual reaction. Facial vision seems thus to be a specified response to a specific acoustic gradient upon which it is based. Remember please in this connection Dr. WILSON's remark: "It is interesting to note that, in the case of the cat, cortical neurones have been found that respond only to certain ranges of changing pitch." Facial vision seems to be the introspective correlate, if we can assume a similar mechanism in man.

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ANATOMICAL AND EXPERIMENTAL OBSERVATIONS ON THE CETACEAN SONAR SYSTEM

by
P. E. PURVES

INTRODUCTION

In view of the anatomical and experimental observations described by FRASER and PURVES (1960) in their study of the accessory air sinuses of the middle ear in cetaceans, the question arises about the manner in which the cetacean voice is co-ordinated with its sense of hearing, and how the emission of sound waves is influenced by the presence of extensive air cavities in the head. It has been proved conclusively by NORRIS et al. (1961) that the smaller Cetacea can find food, avoid obstacles and locate other members of their own kind completely blind-fold, and in so doing, emit, and are sensitive to, underwater sound frequencies of 20 kHz to well over 100 kHz. The wave-lengths of these high frequencies are small relative to the linear dimensions of the air spaces so that whatever the original source of the emitted sound, the vibrations must be subject to such phenomena as reflection, diffraction, interference, resonance, etc., during their passage through the head, with the net result of modifying the polar distribution of the sound field in the ambient water. The far field would of course differ markedly from the near field, because of the greater attenuation of high frequency waves in water.

A great deal of speculation has arisen about the mechanism of phonation, and a number of different hypotheses have appeared in the literature. Some authors, notably KELLOGG (1961), EVANS and PRESCOTT (1962), NORRIS (1964), EVANS et al. (1964), locate the sound producing mechanism among the various pneumatic chambers which are to be found in the upper part of the blow-hole, but others, LAWRENCE and SCHEVILL (1965) and GRIFFIN (1966) believe the sound source to be laryngeal. LILLY (1961, 1962) who carried out an exhaustive analysis of cetacean noises under ideal conditions maintains

that there are at least two, and possibly three sound-producing mechanisms which may be used separately or simultaneously. In his earlier papers he is inclined to the view that these systems are located in the upper nasal chambers, but in his book "Man and Dolphin" he concedes that the larynx may also be involved.

When one recalls the great variety of noises which may be elicited by simply blowing air through the nasal passages of a dead cetacean, it would not be surprising to discover that an intelligent animal like a dolphin could make use of the sound producing properties of its valves and air chambers to produce airborne "humanoid" noises for communication with Man, and in certain circumstances, with its own species. It is evident, however, that the so called separate "layers" of the muscle systems which control the air sacs and valves can only be operated in sequence and not independantly of one another. All the blood vessels and nerves which supply the major groups of muscles spring each from a separate main trunk and pass from layer to layer within the group, branching only within the "layer" of the muscle. This may be demonstrated by injecting the system with latex or polyester resin, where upon the "layers" become quite inseparable owing to the numerous interconnecting vessels. The shearing stresses involved in independant action of the muscle "layers" would be bound to cause rupture of the vessels and nerves.

LAWRENCE and SCHEVILL (loc. cit.) have demonstrated most elegantly that all the various air-sac systems are necessary for the non-muscular occlusion of the blow-hole during submergence, but it can be shown that they are also necessary for the retention and recirculation of air during phonation without themselves necessarily being involved in the production of sound.

This paper is primarily concerned with Sonar and it is proposed to show that Phonation by the larynx is quite adequate to meet the requirements of accurate echo-location. The normal mechanism of phonation in mammals is located in the larynx and the fact that there are no vocal chords of the conventional type in the cetacean larynx has brought about its immediate

rejection as a possible sound source. However, as NEGUS (1949) has shown, Man is one of the few mammals which phonate by means of true vocal chords the majority employing modifications of the thyroarytenoid fold, and a few, the artiodactyl ungulates, of the aryepiglottic folds. It has been our experience that whatever structure is responsible for a certain function in terrestrial mammals, is also responsible for that function in cetaceans, except that the structure may have undergone profound modification for operation under water. Situated as it is, directly between the peribullary air spaces, the glottis is partially acoustically isolated from the ears, and thus in a favourable position for the role of sound emitter. In echolocation, the voice must necessarily be mainly monitored on the echo, rather than on the emitted pulse, if the repeat-frequency is to be correctly adjusted for range. It is, therefore, essential that no unattenuated sound path from emitter to receiver should be available.

Acting on the assumption that the larynx was the main sound emitter we, (F.C.F. and P.E.P.), carried out experiments concurrently with our research on the sense of hearing, on the propagation of laryngeal sound through the head in dead, fresh specimens of Phocaena phocaena and Lagenorhynchus cruciger. In 1962 I was able to repeat these experiments on two more specimens of Phocaena and on the Bottle-nosed dolphin Tursiops truncatus. In 1963 I had the opportunity to compare the results of all these experiments with results of other experiments carried out on live specimens of Tursiops at the Communications Research Institute, Miami, U.S.A. in which the animal's own natural voice was monitored. The account which follows, therefore, is given in the reverse order of that which was employed in the study of the sense of hearing by FRASER and PURVES (loc. cit.), for other parts of the anatomy. A description is first given of the experiments and their results, secondly a delineation of the anatomical features involved, and finally, an interpretation of the mechanism of phonation and echo-navigation.

MATERIALS AND METHODS

The first experiment was carried out on a fresh specimen of the Common Porpoise, Phocaena phocaena, which had been caught accidentally by fishermen in the North Sea. For the purpose of the experiment a variable-pitch, Galton whistle commensurate with the larynx was adjusted to 20 kHz, and attached to an air line, which was then introduced into the trachea until the body of the whistle lay in the rima glottidis with the case between the arytenoid cartilages, figs. 1 and 2. The whistle was considered to be necessary since the mere act of blowing air through the larynx without the whistle produced non-specific noises in many parts of the respiratory tract which could not be monitored satisfactorily. The introduction of electrical devices for the production of sound in the larynx inevitably produces capacitance effects which are distributed with equal intensity over the whole body as MACKAY (1964) discovered to his advantage during his experiments on ingested micro-transmitters in Tursiops. It was found that an air pressure equivalent to 25 mm Hg was sufficient to produce an intense and extremely high-pitched, but audible tone, after the incision had been tightly sutured round the air line. Owing to the self-sealing action produced by inflation of the tubular air sacs, as described by LAWRENCE and SCHEVILL (loc.cit.) a sustained note could not be maintained by this method for more than 20 secs, so that the lips of the blow-hole had to be kept apart by tubing during a prolonged series of measurements. The sound intensity at various points on the head was found by measuring the longitudinal vibration of a suture needle inserted alternatively superficially and deeply at these points. A piezoelectric cartridge was placed so that the stylus rested on the eye of the needle at right angles to its axis, fig. 3, and the output of the crystal was connected to a cathode-follower, amplifier, voltmeter and oscilloscope, fig.2. The lowest voltage after amplification (0.1v) was used as the reference in recording intensity levels in db.

At this stage it should be pointed out that these experiments differ fundamentally from those described by EVANS and PRESCOTT (loc.cit.).



Fig. 1 : X-Ray photograph showing position of a whistle in the larynx of a Common porpoise Phocaena phocaena.

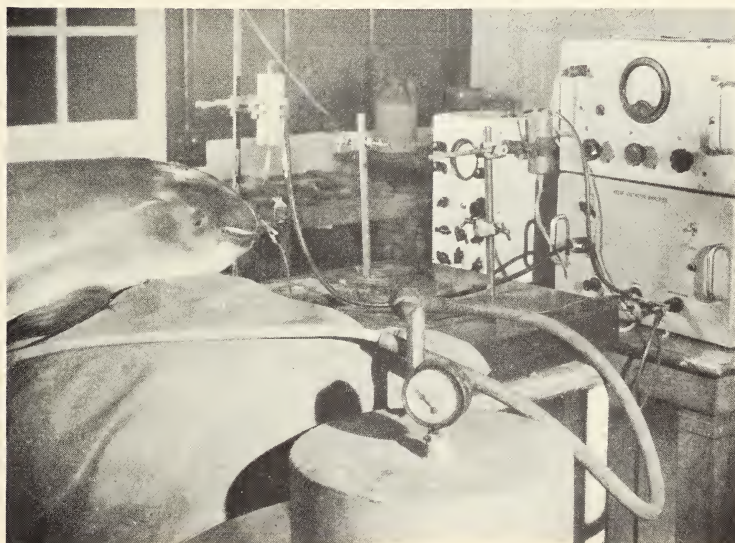


Fig. 2 : Apparatus for the production and measurement of sound vibrations in the head of a Common porpoise Phocaena phocaena.

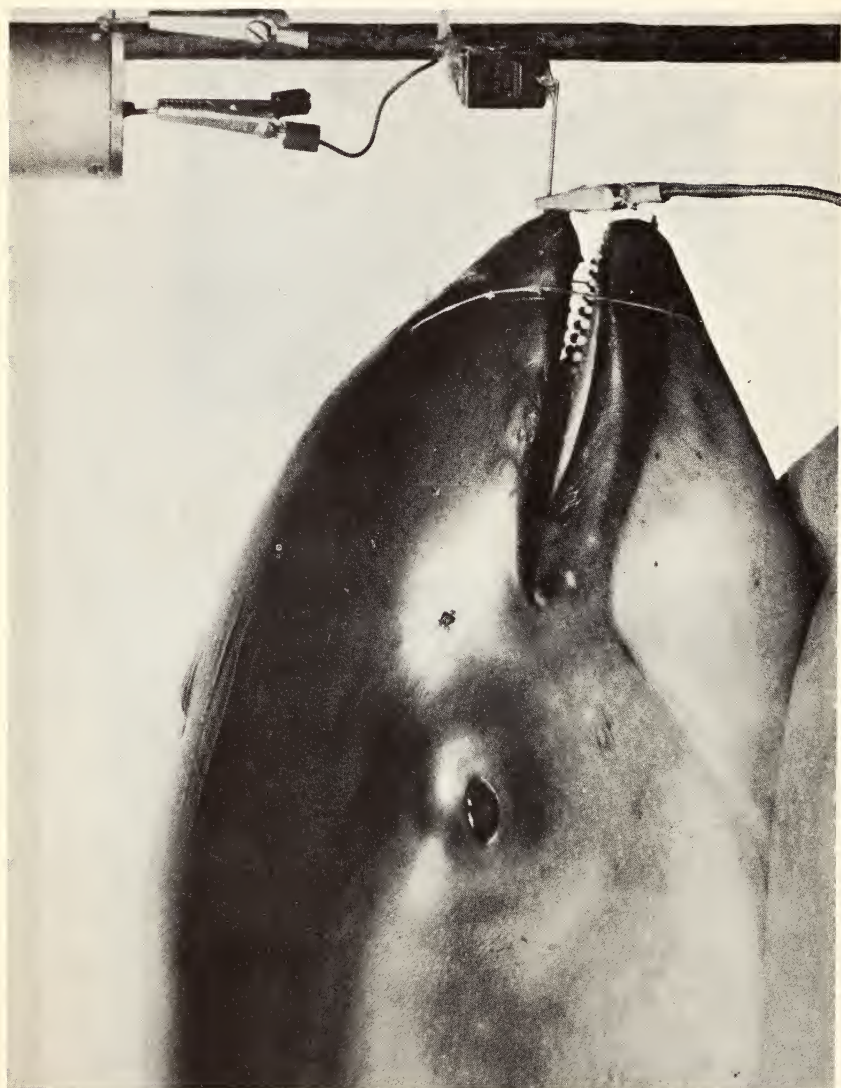


FIG. 3 : Head of Common porpoise *Phocaena phocaena*
showing method picking up sound vibrations.

These authors measured the sound produced by blowing air through the respiratory passages of separated heads of Stenella and Tursiops, using a ring of condenser microphones placed round the head and separated from the surface of the skin by an air-gap of alternatively 0.25 and 15 inches. In these circumstances, because of the large acoustic mismatch between the animal tissues and the surrounding atmosphere most of the energy of the small displacement-amplitude vibrations would undergo internal reflection, so that only the large amplitude vibration of the tissues surrounding the air-sacs would be measured. It is not surprising therefore, that the sound energy showed an asymmetrical pattern consistent with that of the air-sacs. It was not the purpose of our experiments to measure the intensity of vibration of air in the nasal passage but that of the small displacement-amplitude, high energy vibrations transmitted through the body of the whistle to the cartilages of the larynx, assuming these to be further transmitted to the vomer and via the palatopharyngeus muscles to the maxillary bones of the skull. Such measurements required that there should be no large acoustic mismatch at any point. The vibrations of the animal tissues were, therefore, coupled directly to the piezoelectric cartridge via the suture needle.

The experiments of EVANS et al.(loc.cit) bear a closer relationship to reality since they were conducted with specimens under water. These authors were able to demonstrate that the architecture of the skull endows it with definite directional properties as a sound-reflector but they do not show that it is also a good transmitter. In these experiments small sound sources were implanted in the "areas" of the nasal sacs and larynx but the exact location of the laryngeal implant is not stated. It was found that most of the energy of the laryngeal implant was reflected downwards, a result which is not surprising in view of the wide distribution of air cavities on the base of the skull and in the larynx itself. As will be shown later, there is good acoustic coupling between the upper cartilages of the larynx and the bones of the skull so that had the implant been placed within the actual rima glottidis, a different result might have been obtained.

TABLE I - Phocaena phocaena

Horizontal Plane		db		Sagittal Plane		db	
Position		S	D	Position		S	D
2 cm. above eye		6	6	2cm. anterior to blowhole		.13	1.6
4 cm. anterior to eye		.78	6	"		.13	23.4
8 cm. "	"	.6	6	"		.13	6 ⁺
12 cm. "	"	.6	7.8	"		.78	2.0
16 cm. "	"	.13	9.4	"		1.2	20
20 cm. "	"	0	15				
Tip of snout		15.4	23	Tip of snout		23	23
S = Superficial		D = Deep		+ = Premaxilla			

Table showing distribution of sound intensity levels in the head of a Common porpoise Phocaena phocaena radiated from an artificial source in the larynx.

TABLE 1 (Continued) - Phocaena phocaena

Lower Jaw	db	
	S	D
Position		
2cm. below eye	.2	1.2
4cm. anterior to eye	.2	.2
12cm. " " "	0	0
16cm. " " "	0	0
16cm. " " "	0	0
20cm. " " "	0	0
Tip of Lower Jaw	0	0
S = Superficial		D = Deep

Table showing distribution of sound intensity levels in the head of a Common porpoise Phocaena phocaena radiated from an artificial source in the larynx.

The figures for the first experiment with Phocoena phocoena are given in Table I.

Almost immediately afterwards, a deep frozen specimen of Lagenorhynchus cruciger was received in absolutely fresh condition from Dr. C.E. ASH a Whaling Inspector aboard the Balaena. The experiment was repeated in the same way as with Phocoena. The results for Lagenorhynchus cruciger are given in Table II.

Inspection of the figures shows that:

- (a) Maximum values were obtained from the tip of the snout, notwithstanding that this point was furthest away from the source of sound.
- (b) The maximum value is the same in both species despite the fact that the length of the head of L. cruciger is almost double that of P. phocoena.
- (c) The superficial values are very much lower than those measured with the needle in contact with bone, except in the regions where the soft tissues were relatively thin, i.e. in the region just anterior to the eye, the hardpalate and at the tip of the snout.
- (d) Relatively large signals were obtained in the vicinity of the vomer.
- (e) Negligible signals were recorded on the lower jaw.

The very low intensities recorded from the superficial structure of the head could be accounted for in a number of ways. Firstly, by mechanical slip in the suture needle. Secondly, by the presence of bubbles of gas decomposition in the tissues, and, thirdly, by a very low sound transmission from bone to blubber. In order to investigate this problem, the severed head was placed in a large tank of water and the pressure in the air line adjusted so that it exceeded the hydrostatic pressure by about 25 mm. Hg. Under these conditions the whistle continued to function in the larynx. A delicate hydrophone was then moved about at approximately 1 cm distance from the surface of the head and the output monitored visually with the oscilloscope. As in the previous experiments, the maximum response was obtained in the region of the tip of the snout,

but no signal at all could be obtained from near the surface of the melon, nor from other surface covered by a fair thickness of blubber. At a point half way along the gape, the oscilloscope display could be made to appear and disappear by simply opening or closing the mouth.

A section of blubber was then stripped from the throat opposite the larynx, and the hydrophone placed near the surface of the musculature. Signals of moderate strength were again obtained, although the muscle at this point was about 10 cms in thickness. During these experiments it was found that the walls of the resin-bonded, chopped fibre-glass tank, were practically anechoic for the strength of signal used. The general inference from these experiments was that the poor signals obtained from the superficial layers of the head were not due to mechanical slip of the suture needle but to some factor disturbing the transmission of sound from muscle and bone to blubber, a phenomenon which was commented upon by PURVES (1966). If this factor was the presence of gas bubbles, then blubber must be more prone to the formation of bubbles than bone and muscle. There was also an indication that sound transmission to the lower jaw was blocked near its articulation to the skull.

Some time later, whilst carrying out economic work at the Zoological Laboratory, Amsterdam, I was able to repeat the experiments on two more specimens of Phocaena and on a Bottle-nosed dolphin Tursiops truncatus, but no superficial readings were taken at this time. When the first experiments on Phocaena was performed in Amsterdam, completely negative results were obtained, and the animal was taken away for autopsy.

On removing the flesh from the skull, it was found that the rostrum had been fractured completely through its base and was detached from the remainder of the skull. Another specimen was then experimented upon and the results were almost exactly as those obtained in London.

The results obtained from Tursiops were in general, similar to those obtained in Phocaena but in this experiment a more sensitive cartridge was used, a fact which may account for the higher voltages obtained. The results for Phocaena and Tursiops are given in Tables III and IV.

TABLE II - Lagenorhynchus cruciger

Horizontal Plane		db		Sagittal Plane		db	
Position		S	D	Position		S	D
2 cm. above eye		3.3	5	4 cm. anterior to blowhole		.3	15
4 cm. anterior to eye		1	12	"		0	0
12 cm.		.75	11	"		0	21.5
16 cm.		.75	10.25	"		0	21
32 cm.		.3	11	"		0	21
Tip of Snout		23	23	Tip of Snout		23	23
S = Superficial				D = Deep			

Table showing distribution of sound intensity levels in the head of a Crucigerous dolphin Lagenorhynchus cruciger radiated from an artificial source in the larynx.

TABLE II (Continued) - Lagenorhynchus cruciger

Lower Jaw	db	
Position	S	D
2 cm. below eye	O	O
4 cm. anterior to eye	O	O
12 cm. " " "	O	O
16 cm. " " "	O	O
32 cm. " " "	O	O
Tip of Lower Jaw	O	O
S = Superficial	D = Deep	

Table showing distribution of sound intensity levels in the head of a Crucigerous dolphin Lagenorhynchus cruciger radiated from an artificial source in the larynx.

TABLE III - Phocaena phocaena

Horizontal Plane	db	Sagittal Plane	db	Lower Jaw	db
2 cm. above eye	11.25	2 cm. anterior to blowhole	16	2 cm. below eye	0
4 cm. anterior to eye	11.75	4 cm. "	12	4 cm. anterior to eye	0
8 cm. " "	12.5	8 cm. "	16.5	8 cm. " "	0
12 cm. " "	15.5	12 cm. "	21.5	12 cm. " "	0
16 cm. " "	15.5	16 cm. "	21.5	16 cm. " "	0
20 cm. " "	21.75	20 cm. "	20.75	20 cm. " "	0
Tip of Snout	23.0	Tip of Snout	23.0	Tip of Lower Jaw	0

Table showing distribution of sound intensity levels in the head of a Common porpoise Phocaena phocaena radiated from an artificial source in the larynx.

TABLE IV - Tursiops truncatus

Horizontal Plane	ab	Sagittal Plane	db	Lower Jaw	db
Opposite ear	0			Below ear	0
4 cm. anterior to ear	0			4 cm. anterior to ear	0
3 cm. above eye	12.5			3 cm. below eye	1.5
4 cm. anterior to eye	6.0			4 cm. anterior to eye	0
8 cm. " " "	12.5	2 cm. anterior to blowhole	25	" " "	0
12 cm. " " "	6.0	4 cm. "	24	" " "	0
16 cm. " " "	13	8 cm. "	23	" " "	0
20 cm. " " "	14	12 cm. "	26	" " "	0
24 cm. " " "	13.5	16 cm. "	28	" " "	0
Tip of Snout	24.0	Tip of Snout	32	Tip of Lower Jaw	0

Table showing distribution of sound intensity levels in the head of a Bottle-nosed dolphin Tursiops truncatus radiated from an artificial source in the larynx.

TABLE IV (Continued) - *Tursiops truncatus*

Hard Palate (Lateral)	db	Hard Palate (Medial)	db
Level with first tooth	8	Mid line level with first tooth	24
4 cm. anterior to first tooth	12	4 cm. anterior to first tooth	44
8 cm. " " "	12	8 cm. " "	44
12 cm. " " "	22.5	12 cm. " "	46
16 cm. " " "	29	16 End of vomer	48
Tip of Snout	23	Between maxillae	12

Table showing distribution of sound intensity levels in the head of a Bottle-nosed dolphin *Tursiops truncatus* radiated from an artificial source in the larynx.

In all cases, there is a tendency both in horizontal sagittal planes for the sound to become more intense towards the tip of the snout but it is of particular interest to note that the sound intensities measured along the central axis of the hard palate are greatest of all.

In August 1963, I spent a week at the Communications Research Institute, Miami, U.S.A., where experimental work is carried out on captive specimens of Tursiops truncatus. In one of the laboratories, the animals were kept in large fibre-glass tanks, each having a narrow Plexiglass annex as shown in figs. 4 and 5. When the tanks were first installed in 1961, the animals were driven into these annexes for the purpose of making psychological and cathode-ray encephalograph studies, but since that time had been in the habit of entering them voluntarily, spending a great deal of time observing the activities of people in the laboratory. They were also able voluntarily to back out of the annexes into the main tank if they so wished. This arrangement was ideal for my purpose, as it enabled sound intensity experiments to be carried out without having to restrain the animals in any way and without the use of hydrophones.

A pair of flat-faced barium titanate transducers 1 cm square were clamped to the walls of the annex fig. 5 and coupled acoustically to the Plexiglass by coating with a thin film of petroleum jelly. The transducers were then connected by long, concentric, earthed cables to two identical band-pass filters, preamplifiers, and a double-beamed oscilloscope which were enclosed in an instrument booth out of sight of the animal. One transducer was fixed to the end of the annex, and coupled to the upper trace of the oscilloscope and the other to the side, at a point approximately in line with the glottis and posterior nares of the animal when it was fully in the annex. This transducer was coupled to the lower trace of the oscilloscope.

The mere activity of fixing the apparatus was sufficient to excite the animals curiosity and it would enter the annex emitting bursts of sonar activity at the same time. The emitted sounds were of three main types, a clicking pulse of variable repeat-frequency, short or sustained whistles, and loud squawks. During the last two types of phonation, a considerable amount of noise was emitted from the blow-hole into the air, if the former happened to be out of water at the time. It should be pointed out at this

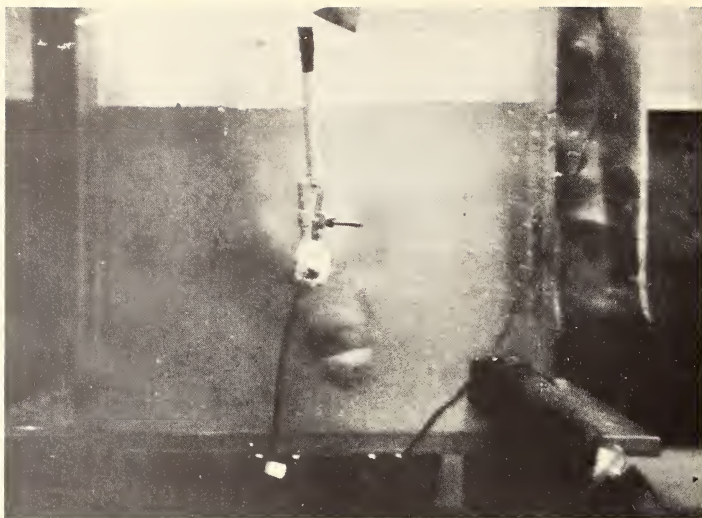


Fig. 4 : A living specimen of Bottle-nosed dolphin Tursiops truncatus in a Plexiglass annex with transducer fixed to the outside of the tank.

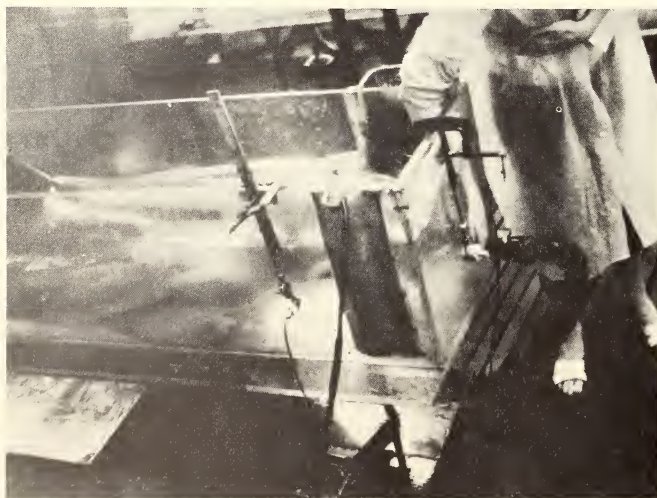


Fig. 5 : A living specimen of a Bottle-nosed dolphin Tursiops truncatus with barium titanate transducers fixed to the outside of the tank.

stage, that it is the latter phenomenon which may have led to the assumption by a number of authors that the noise emitter is the blow-hole mechanism. However, it is easy to be misled in this respect. In the laboratory experiments on the dead animals, previously described, the sound of the whistle seemed to come from the blow-hole, notwithstanding that the whistle was located deeply in the larynx. It is significant also that the dolphins could emit all these noises with equal facility, though with less intensity, when the blow-hole was closed and the head completely submerged.

The filters were set to pass frequencies above 30 kHz since the transducers were relatively insensitive below this level. The photographs shown in figs. 6-12 were taken with a polaroid camera manually operated. Fig. 6 shows the trace set at 10 Hz on the oscilloscope with the animal just entering the annex at a distance of 1,5 metres approximately. The repeat frequency is, therefore, 80 pps. It will be seen that the amplitude on the upper trace is greater than that on the lower, the measured voltages being 0.12 v and 0.04 v respectively; difference 9.6 db approximately. The effect of a greater amplitude on the upper trace might have been expected irrespective of any directionality of the pulse owing to the channelizing effect of the annex and the angle of reflection at the side transducer. Fig. 7 shows the trace set at 100 Hz when the animal was nearly touching the end of the annex; the repeat frequency is 300 pps. and the voltage strength on the upper and lower traces 0.28 v and 0.09 v respectively, difference 9.8 db. Since the camera exposure was 0.04 sec each pulse shown on the photograph represents a group of approximately 4 clicks superimposed. As might be expected at this repeat frequency, individual clicks could not be distinguished by ear, the general effect being that of a fairly high-pitched squawk. In this last position the distance from the sound producing mechanism, (whether it be the larynx or the nasal passages) to the end transducer, was at least four times that to the side transducer, and yet the amplitude of the sound at the end transducer was approximately 9 db above that at the side transducer. This result showed that all

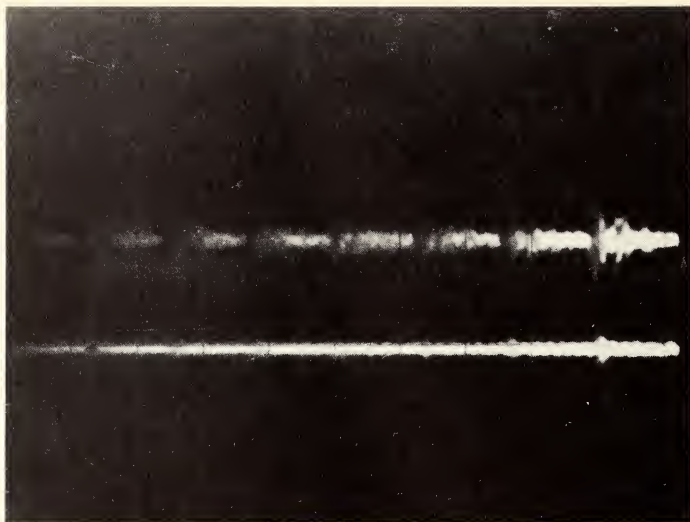


Fig. 6 : Oscilloscope traces of sonar clicks from a
Bottle-nosed dolphin Tursiops truncatus.
Repeat frequency 80 pps voltage ratio
0.12 to 0.04. Difference 9.6 dB approx.

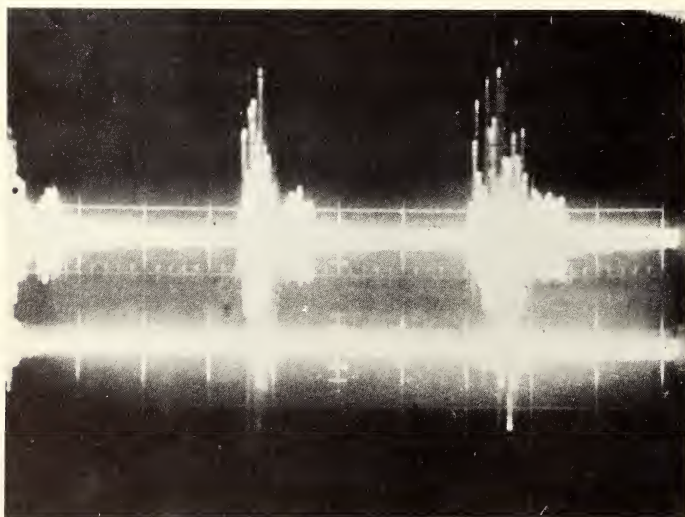


Fig. 7 : Oscilloscope traces of sonar clicks from a
Bottle-nosed dolphin Tursiops truncatus.
Repeat frequency 300 pps voltage ratio
0.28 to 0.09. Difference 9.8 dB approx.

frequency components above 30 kHz were being beamed predominantly forward along the rostrum. The absence on the lower trace of the double pulse should be noted.

No frequency analyser was available at this time but it was of some interest to find out whether there were any frequency components (above 100 kHz) in the clicks which could be expected to be fairly sharply directional. Fig. 8 shows the oscilloscope trace set at 50 kHz with the animal near the end of the annex. There are six superimposed clicks with three complete sine waves in each, indicating a frequency component of 150 kHz. The peak voltage on the upper trace was 0.26 v but no useful voltage was measured on the lower trace, a result indicating fairly sharp directionality. In order to obtain a qualitative picture of the limits of the sound field at this frequency, both transducers were placed at the end of the annex, separated by a distance of 20 cms. The result is shown in fig. 9. The peak voltage on each trace is 0.09 v approximately, i.e. the same voltage as was obtained from the side transducer placed directly opposite the larynx. At distances further apart, no useful voltages could be obtained.

During this experiment it was found that the animal could be made to point its snout between the transducers or at either transducer by placing the hand inside the tank as shown in fig. 5. and by moving the fingers to the required position. Every time the snout pointed at a single transducer the oscilloscope picture reverted to that shown in fig. 8. By this means it was possible for the observer in the instrument booth to call out the position of the snout without himself being able to see the animal. It will be noticed that only three clicks appear on each trace in fig. 9 whereas there are six in the upper trace of fig. 8. A number of explanations could be given for this phenomenon but my submission is that the fig. 9 represents two trains of clicks, one from each side of the rostrum and that fig. 8 represents a summation of these two trains at the tip of the rostrum, the individual clicks being slightly out of phase with each other.

Fig. 10 shows a large number of 150 kHz sine waves on the upper trace when

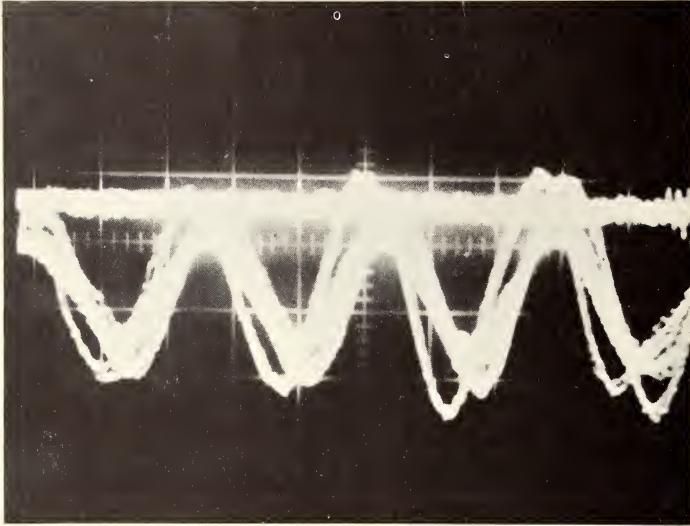


Fig. 8 : Oscilloscope trace of the ultrasonic component
of sonic activity of Bottle-nosed dolphin
Tursiops truncatus 150 kHz voltage ratio
0.26 V to 0.

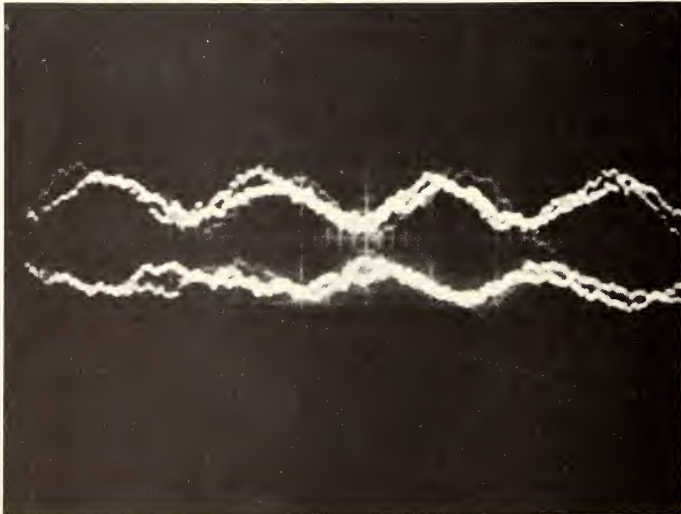


Fig. 9 : Oscilloscope trace of the ultrasonic component
at sonic activity of a Bottle-nosed dolphin
Tursiops truncatus 150 kHz voltage ratio
0.09 - 0.09.

one transducer was placed 20 cms vertically above the tip of the snout and level with the top of the melon, the other transducer being disconnected. Fig. 11 shows an even larger number of 150 kHz sine waves of greater amplitude when the transducer was lowered to the tip of the snout, the voltage readings being 0.16 and 0.28 respectively, difference 4.9 db approximately. Fig. 12 shows two sets of 150 kHz sine waves when the two transducers were placed 20 cms apart, 20 cms vertically above the rostrum. The voltage reading on each being 0.09 volts, exactly as before. The combined set of readings indicate that at this high frequency, although a considerable amount of sound energy was being directed vertically, there was very little lateral spread and that by far the greater amount of energy was located at the tip of the snout. During this last experiment the animal emitted no audible signal but the observer stated that he could distinctly feel the vibration when his hand was placed in the tank in front of the snout. The great reduction of energy in the lateral plane strongly suggests interference phenomena from two sources horizontally separated.

A final experiment consisted of coupling a transducer to the bottom of the annex and moving it forward in stages towards the tip of the lower jaw. No measurable voltages could be obtained. All these photographs had to be taken just a few hours before I was due to leave the laboratory so that there was insufficient time to take a complete set of readings at various points as in the whistle experiments. Insufficient data about camera exposure times and amplification settings were recorded to provide accurate quantitative information about the sound energy levels at the various points. However, the photographs do show that both in the whistle experiments on dead animals and in the experiments on live animals using their own, natural voice, the qualitative results are very similar. It is appreciated that all the recorded results are near-field effects in close contact with the animal and in the higher frequency range but they were collected in order to try to determine the possible source of the sound emission. The high concentration of energy at the tip of the snout will have to be accounted for on anatomical and physical grounds and it is from this standpoint that

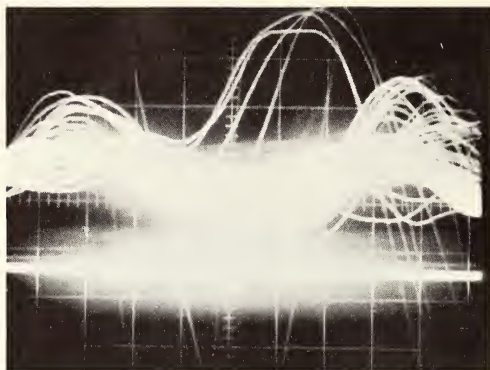


Fig.10



Fig.11

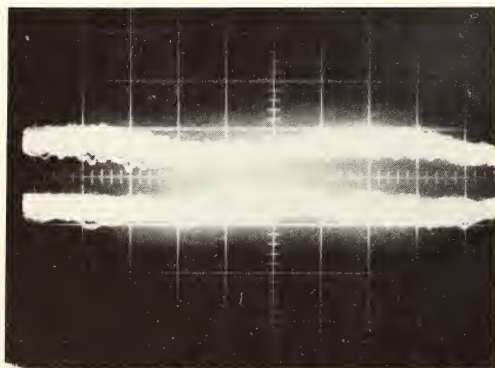


Fig.12

Oscilloscope traces of the ultrasonic component
at sonic activity of a Bottle-nosed dolphin
Tursiops truncatus 150 kHz at tip of snout.

the two main possible sound sources, the larynx and the blow-hole mechanism, will be discussed in the rest of this paper.

THE STRUCTURE OF THE LARYNX

Since TYSON (1680) first described the larynx of the Common Porpoise Phocaena phocaena a great number of anatomists have interested themselves in the cetacean vocal organ, and at the present time the larynges of very few genera remain to be described. MURIE (1870,1873), POUCHET and BEAUREGARD (1889), D'ARCY THOMPSON (1892), RAWITZ (1900), BOENNINGHAUS (1902), SCHULTE (1916), KERNAN and SCHULTE (1918), HOSOKAWA (1950), KLEINENBERG and YABLOKOV (1958), BROWN (1962).

For this reason it is not proposed at this time to enter into a detailed comparative study, but to give a general account of those structures which are well known, and a more detailed description of those parts which have not been adequately studied, but which are relevant to the subject of this paper.

The general form, fig. 13 is typically mammalian and consists of a skeletal framework of cartilages, held together by ligaments, muscles and mucous membranes. It is possible to identify all the main structures by the names applied to their homologues in human anatomy, and in describing the modifications that have occurred, the larynx of Man will be taken as a reference.

The most striking difference in the form of the cetacean larynx from those of all other mammals lies in the structure of the glottis, which is in the shape of an elongated spout. The distal end of the spout, the axis of which is orientated anterodorsally to that of the rest of the larynx, is inserted into the posterior nares figs. 14 and 15. Much confusion has arisen in the interpretation of the structures inside the larynx, owing to an assumption that the dorsal inclination of the glottis, fig. 15 (GLO) is a secondary development, correlated with the dorsal situation of the blow-hole (BLO). In fact, dorsal orientation of the glottis is a feature common to most mammals, and it is the horizontal orientation of the trachea (TRA) cricoid and thyroid (CTH) cartilages, which is the secondary

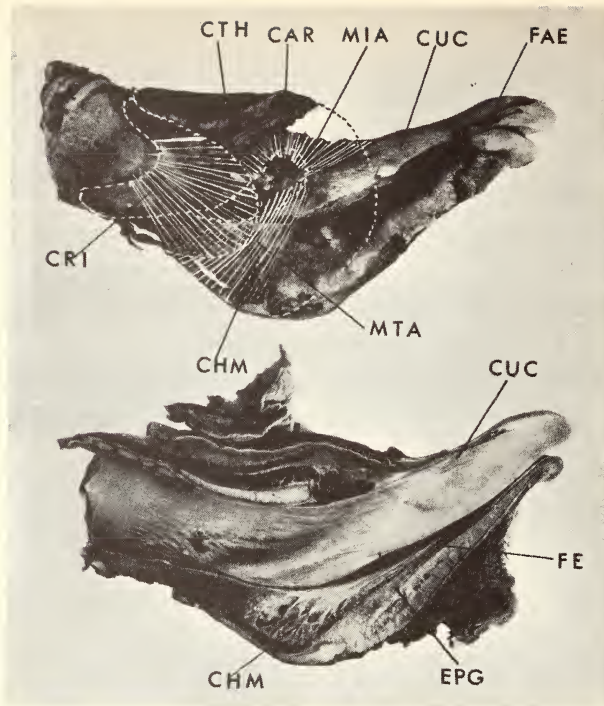


Fig. 13 : Laryngeal cartilages of a Common dolphin Delphinus delphis.

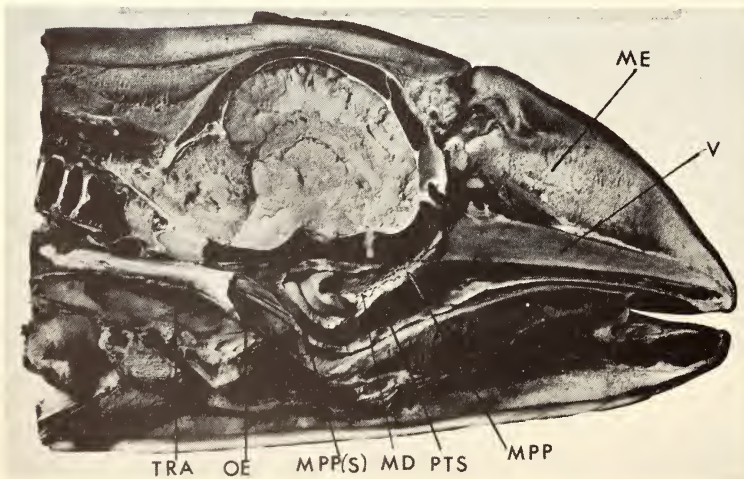


Fig. 14 : Sagittal section and dissection of larynx of a Common porpoise Phocaena phocaena.

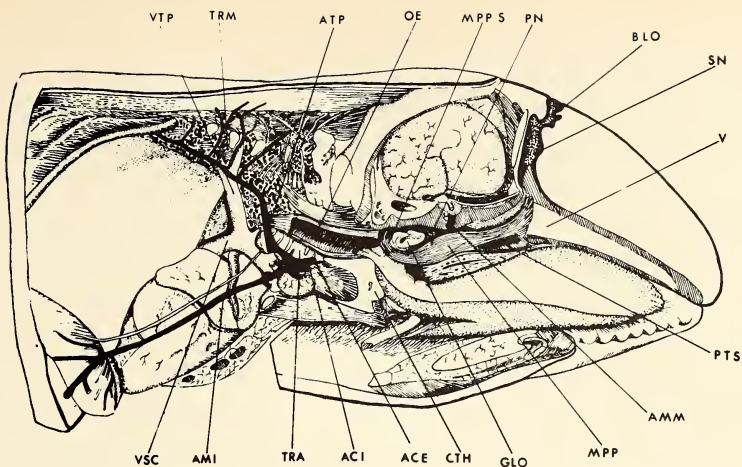


Fig. 15 : Dissection of the head and thorax of a 3 ft. foetus of False Killer whale *Pseudorca crassidens*.

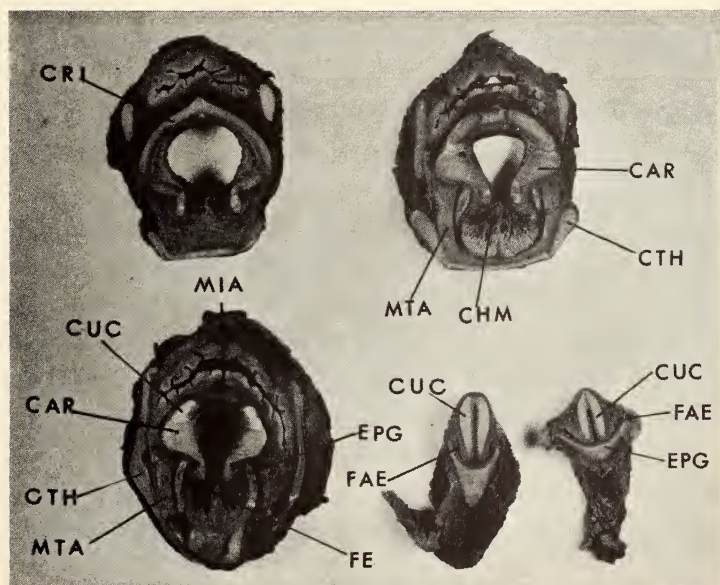


Fig. 16 : Transverse sections of the larynx of a Common porpoise *Phocaena phocaena*.

development, due to shortening of the neck and respiratory tract. The sharp horizontal inclination of the respiratory tract at the level of the thyroid cartilage has caused the arytenoids, figs. 13 and 16 (CAR) to be more closely intruded into the thyroid angle, so that the thyroarytenoid muscles, figs. 13 and 16 (MTA) are relatively short compared with those of other mammals of comparable size. For the same reason the cricoid (CRI) is partially telescoped over the arytenoids and the ligamentous attachment is greatly augmented, so that the arytenoids are not free to rotate on the cricoid as in terrestrial mammals.

In the angle of the thyroid cartilage and between the two thyroarytenoid muscles a remarkable system of bilaterally symmetrical air chambers, figs. 13 and 16 (CHM) lined by mucous membrane and mucoid tissue, completely fills the vocal part of the rima-glottidis, isolating the thyroarytenoid muscles from the latter. Thus there are no vocal folds nor vocal chords of the type found in terrestrial mammals. These pouches end in blind diverticulae posteriorly but continue anteriorly as far as the base of the epiglottis (EPG) where they break into a symmetrical arrangement of high, longitudinal folds, fig. 13 and 16 (FE) formed the mucous lining of the epiglottis. The base of the epiglottis, fig. 16 (EPG) is also curiously modified, taking the form of a deep trough, the lateral walls of which reach posteriorly well beyond the anterior borders of the arytenoid (CAR) and cuneiform (CUC) cartilages and enclosing the system of epiglottis folds, described above. Because of this arrangement, the aryepiglottic folds (FAE) are deep, extremely narrow and supported both mesially and laterally by stiff cartilage. More distally, in the upper portion of the epiglottic spout, the longitudinal folds become gradually narrower and less elevated, until only the medial fold remains. The greater part of the epiglottic trough in this region is filled by thick, hyaline cartilage. In the Ziphioid whales, the medial fold is also replaced by cartilage. Anteriorly to the cricoid, the fused arytenoid and cuneiform cartilages, which, with the interarytenoideus muscle, form

the posterior boundaries of the epiglottic spout, become more and more approximated to each other and to the trough of the epiglottis, so that the anterior part of the rima-glottidis tapers gradually until, at the distal end of the spout, it remains only as a minute aperture. Where all three cartilages touch, the mucous lining is perfectly smooth, so that when the glottis is constricted, no interval remains between them. If the epiglottic spout of any odontocete larynx is cut into transverse sections from the base upwards, the morphological arrangement of the epiglottic folds, described above, can be seen clearly, fig. 16. In the region of the air chambers, the medial fold is but slightly elevated, so that the interval between the anterior borders of the arytenoid cartilages is fairly wide. At the level of the base of the epiglottis, the medial fold is very high and completely fills the arytenoid interval. At this point it is also flanked by two less prominent, tapering folds, (the vocal folds of MURIE) and a number of shallower folds. As the medial fold is traced up the epiglottic spout it is found to follow the contours of the anterior borders of the cuneiform cartilages (CUC) exactly, filling the interval between them.

By the whole arrangement described above, the upper part of the rima-glottidis can, when the glottis is constricted, be divided into three narrow channels, one lying between the cuneiform cartilages and the other two, bounded by the epiglottis, cuneiform cartilages and aryepiglottic folds. At the very apex of the epiglottic spout the cuneiform cartilages taper abruptly and become embedded in two rounded bosses of yellow elastic tissue. The epiglottic cartilage widens laterally into a flange, figs. 14, 15 and 16, which curls posteriorly and dorsally, partially embracing the cuneiforms, to which it is joined by the lateral aryepiglottic folds (FAE).

Notwithstanding the extreme complexity of the air sac system, and its associated epiglottic folds and cartilages, the whole assembly is remarkable for its bilateral symmetry, so that when the epiglottis is con-

stricted and air blown through the trachea, the larynx expands in a perfectly symmetrical manner. Owing to the thin, membranous nature of the folds and the posterior operculation of the pouches, a system of anteriorly directed valves operates to drive the contained air forward up the glottis when the larynx is constricted by manual pressure.

THE STRUCTURE OF THE NASO-PHARYNX

As previously stated, the tip of the epiglottic spout is inserted into the posterior nares. At this point it is embraced by the palatopharyngeal sphincter and the arcus palatinus, figs. 14, 15 and 17 (MPP, I). Owing to the sharp, horizontal flexure of the respiratory tract (TRA) and the intranarial situation of the epiglottic spout, the pharynx and oesophagus (OE) are orientated posterodorsally from the oral cavity, so that nearly the whole of the arcus palatinus surrounds the posterior nares, and lies within the mesial borders of the palatopharyngeal sphincter. In this position, it is difficult to separate the two sets of muscles, and in dissection it is necessary to trace them from their points of origin. The arcus palatinus commences as two sets of muscles high in the posterior nares, fig. 17, the partes interna, (MPP, I) of the palatopharyngeus being by far the most massive in each set. They originate on the posterior aspect of the palatine bone, and the upper surface on the palatine aponeurosis (PA). Passing postero-ventrally on each side of the vomer, they are in relation to the nares (PN) posteriorly and to the pterygoid bones and their air spaces, (PTS), anteriorly, laterally and ventrally. Below the nares, the fibres of each muscle decussate both dorsally and ventrally and surround the epiglottic spout, forming a deep semi-circular recess (SRC) into which is inserted the lips of the epiglottis and lateral aryepiglottic folds. The partes externa, see FRASER and PURVES (loc.cit) of the palatopharyngeus originate more ventrally on the palatine aponeurosis and descend in company with the partes interna. Below the nares they also decussate dorsally and ventrally and with the superior constrictor (MSC)

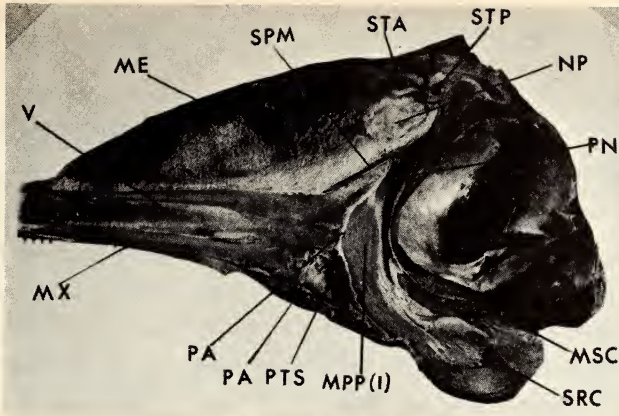


Fig. 17 : Sagittal section of the head of a Common dolphin Delphinus delphis with palato-pharyngeal muscle mass.

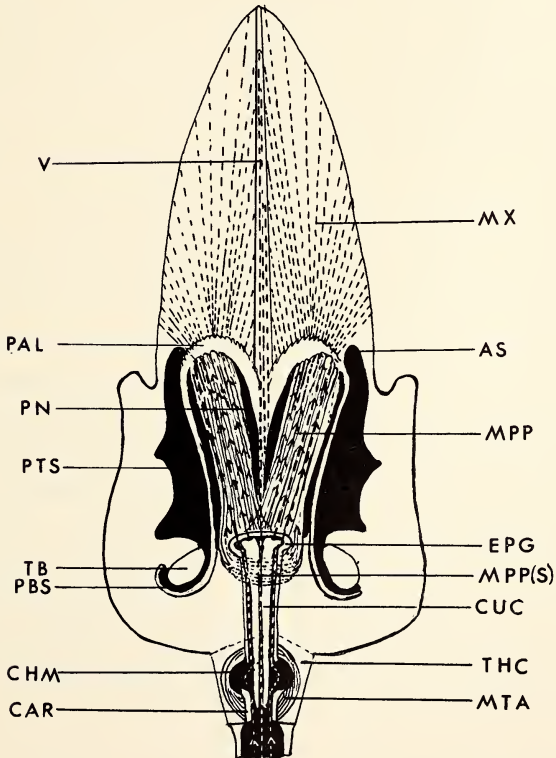


Fig. 18 : Schematic drawing of skull and larynx of an Odontocete cetacean showing probable distribution of sound energy.
 White areas = bone black areas = air spaces.
 White dotted lines = air pathways.
 Black dotted lines and arrows = sound pathways.

form part of the dorsal and external rim of the palatopharyngeal sphincter. It is obvious that the partes interna of the palatopharyngeus referred to above, corresponds to the pterygopharyngeus of LAWRENCE and SCHEVILL (loc.cit.) and that the partes externa corresponds to their palatopharyngeus. If these names are to be assigned to the separate parts of the palatopharyngeus, I prefer to reverse the order and refer to the partes interna as the palatopharyngeus since it clearly originates on the palatine bones. The partes externa on the other hand originates on the posterodorsal aspect of the pneumatized pterygoid bones and is, therefore, more properly called the pterygopharyngeus. From the functional point of view this distinction is important, since the acoustic coupling of the palatopharyngeus with the bony rostrum is very good, whereas that of the pterygopharyngeus is poor because of its contiguity with the pterygoid air spaces. As LAWRENCE and SCHEVILL point out, the partes interna forms the strong sphincter round the tip of the "arytenoepiglottid cartilages". The partes externa is continuous with the "pars thyropalatinus" which inserts between the thyroid and the epiglottid cartilages. It follows, therefore, that the acoustic coupling between the tip of the epiglottic spout and the bones of the rostrum will be good whilst that between the thyroid cartilages and the rostrum will be poor. This phenomenon can be demonstrated experimentally and it implies that noises produced in the lower part of the larynx are not transmitted to the bones of the skull, perhaps for good reason. The anterior portion of the outer sheath of the palatopharyngeal sphincter is largely non-muscular and consists of a strong fibrous band, which is continuous with the palatine aponeurosis along the whole posterior border of the pterygoid hamulae. It sweeps backward, lateral to the levator palati to blend with the inner surface of the superior constrictor muscle fig. 17 (MSC) near its upper border. The mucous lining of the posterior nares, which covers the whole system of muscles, is marked by a regular arrangement of mucous ducts, fig. 14 (MD) whose apertures are directed

posteroventrally towards the palatopharyngeal sphincter. It is important to note that beyond the level of the sphincter the two sets of intra-narial muscles diverge in a symmetrical manner, and are almost wholly enveloped in air spaces. For details of the distribution of these air spaces, reference should be made to FRASER and PURVES (1960) but a general statement can be made here.

The main reason for the intra-narial position of the palatopharyngeal muscle mass is that there is no soft palate in odontocete cetaceans. The pterygoid hamulae are greatly enlarged, being extended posteriorly and anteriorly, and inflated by pneumatic extensions of the middle ear cavity (PTS). Their mesial borders meet along the mid-line, splitting the palatine aponeurosis into dorsal and ventral sheets, fig. 17 (PA), separated by air cavities. The extensions of the middle ear cavity, fig. 18 (PBS) also isolate the ear bones (TB) from the skull and cut deeply into all three sphenoidal regions, so that the air system on each side of the skull is separated from the other only by a narrow, but rigid, strip of bone along the ventral axis of the cranium.

The palatopharyngeal muscles are in relation to these air sac systems on their ventral and lateral aspects, and to the nasal passages on their posterior and dorsal aspects, along nearly their entire lengths. It is only along the central axis dorsally and at the origins of the posterior surfaces of palatine bones that there is no contiguous air space. To complete the general description of the nasopharynx, it must be stated, that as with the larynx, this part of the respiratory tract is perfectly bilaterally symmetrical and in marked contrast with the upper narial region, which in the odontocete is noted for its asymmetry. Even in the Sperm whale Physeter catodon, in which one of the upper nares is from five to seven times greater in diameter than the other, there is not the least trace of asymmetry in the posterior narial region.

THE ARCHITECTURE OF THE SKULL

Although it is appreciated that the minute architecture of the skull is mainly related to the manner of growth of the component bones, it is believed by the author that it also has an important influence on the distribution of sound waves emanating from the larynx, so a brief description is required here.

If the ventral surface of the skull of any odontocete is examined closely, fig. 18, it will be seen that from the arcuate, anterior borders of the palatine bones (PAL) the trabeculae spread fan-wise on the ventral surface of the rostrum and the orbital processes of the frontal bones. A great number of the trabeculae on each side converge on the central axis of the rostrum and would ultimately meet, were it not for the intrusion of the intermaxillary suture and vomer. The trabeculae of the vomer (V) itself are all very nearly parallel with the long axis of the rostrum. Examination of the disarticulated bones of a young specimen shows that the corrugations on the frontomaxillary suture also diverge from the palatine region. In other regions of the skull, particularly those which are contiguous with air spaces, the matrix of the bone appears to be more compact and the trabeculae less uniformly orientated. It is interesting to note too, that the axes of the foramina, distributing nerves and blood vessels to the dorsal surface of the rostrum, all diverge from the palatine region in general conformity with the orientation of the trabeculae.

The internarial, posterior aspects of the palatine bones, fig. 18 (PAL) to which the two sets of palatopharyngeal muscles (MPP) are attached, are concave anteroposteriorly and elongated in a ventrodorsal direction. Their ventral extremities are separated in the Common Porpoise by approximately 2 cms, but diverge dorsally, so that their upper extremities are separated by about 5 cms.

This general form and orientation of the palatine bones is common to all odontocetes, but the lateral separation of the bones varies throughout the order.

THE FUNCTION OF THE LARYNX

In considering the function of the cetacean larynx, it is necessary to take into account the fundamental difference between the mode of propagation of sound in air and water. These differences in the physical properties of sound propagation in the two media were seen to have been of great importance in the interpretation of the modification of structures in the middle ear, see FRASER and PURVES (loc.cit) and it is not surprising that they are also relevant to the understanding of modifications in the larynx.

In all terrestrial mammals, phonation involves the vibration of one or more of a variety of structures, such as vocal folds, vocal cords, thyroarytenoid folds, thyroaryepiglottic folds, etc., which in some cases operate in conjunction with resonant cavities in the mouth and nasal cavities, NEGUS (1949). In every case, air disturbances set up in the vicinity of these structures are propagated directly to the ear of the hearer through the air in the atmosphere. Thus there is no discontinuity of medium between transmitter and receiver, and consequently no loss of energy, except that which accrues from attenuation. In the cetacean, air disturbances of a similar nature would have to be transmitted through solid tissues and the surrounding sea water before reaching the ear of another cetacean. It is well known that where a gas-liquid interface is infinite or semi-infinite in area with respect to the wavelength of an emitted vibration, there is over 99 % reflection of energy at the interface, whether the vibration is initiated in the gaseous or in the liquid medium. This is perhaps the main reason why I believe that air vibrations in the larynx and nasal passages of cetaceans are relatively unimportant, and that phonation does not take place by the operation of any structure involving simple harmonic motion. The general principle seems to involve the mechanical vibrations of the relatively heavy structures of the glottis which are transmitted to the pharyngeal muscles and thence to the bones of the rostrum, and finally to the sea water without change of medium. Other reasons are concerned with the recorded frequencies and qualities of sounds emitted from living cetaceans and of sound produced

artificially in larynges in the laboratory.

It is generally agreed that in Man, the higher pitch of the voice in females is associated with the shorter vocal cords. In the small, head register of the soprano, the notes are produced by vibrations of only the inner margins of the cords, and the vocal chink being reduced to a small anterior aperture, which becomes smaller as the pitch rises. McKENDRICK, according to BURNS (1921), has shown that the limits of performance of the human voice range from FL (85 Hz) in the base to G4 (768 Hz) in the soprano. The larynx of the Bottle-nosed dolphin, Tursiops truncatus is about five times the size of that of Man, and yet the frequencies of the vibrations emitted by these animals lie between the ranges of 5 Hz to 170 kHz, KELLOGG (1953).

The noises emitted by toothed cetaceans have been variously described as being like "the sound of musical glasses when badly played", "a rusty hinge", "creaking gate", "pneumatic hammer", whistling, chirping, clicking, etc., KELLOGG, (loc.cit.) states "one is similarly reminded of the Bronx cheer made by blowing air through tightly pressed human lips". All these noises belong to a particular class of vibration, which VAN DER POL (1926) described as "relaxation oscillations". In all these examples, the frequency is not dependant on the customary ratio of elasticity and mass, as is the case with vibrating reeds and vocal cords, but is controlled by some form of resistance, which, on reaching a certain critical value, suddenly relaxes, builds up again and so on. From mathematical considerations and analogous electrical circuits, VAN DER POL (loc.cit.) has deduced that the periodic time of a relaxation oscillation is typified by the equation:

$$T_{rel} = 1.61 \frac{r}{s}$$

The fundamental period of the vibration is, apart from the numerical constant, defined by a quantity involving resistance (r) and elastic forces (s) only. Summarizing the properties of relaxation oscillations, VAN DER POL states:

- (a) "their time period is determined by a time constant or relaxation time;
- (b) their wave form deviates considerably from the sinusoidal curve, and, as very steep parts occur, many higher harmonics of great amplitude are present;
- (c) a small impressed periodic force can easily force the relaxation system into step with it (automatic synchronisation, even on sub-harmonics) while under these circumstances;
- (d) their amplitude is hardly influenced at all".

It is proposed to show that all these properties are relevant to the production of directional beams of sound initiated in the larynx of toothed cetaceans.

In terrestrial mammals the arytenoid cartilages are normally approximated during phonation by rotating mesially on the cricoid cartilages. The rima glottidis is then further constricted by controlled contraction of the thyroarytenoid muscles (NEGUS 1949). In Man, this involves partial approximation of the vocal cords or thyro-arytenoid folds and it was once thought that when air was passed through the chords they would vibrate harmonically at a pitch determined by the degree of contraction of the muscles.

In a remarkable series of experiments, HUSSON (1962, 1963) demonstrated that the action of a single vibration of the vocal chords could be divided into three well-defined phases. An opening and a closing phase followed by a resting phase during which the current of air was stopped. During the closing phase which can last for less than 0.005 sec, the air current receives a shock wave which raises its velocity to several hundreds of metres per second - frequently to above the speed of sound.

The sound produced at the level of the glottis is not a simple harmonic vibration but a discontinuous series of pressure waves charged with harmonic components up to ten times the fundamental frequency of vibration of the chords.

That the discontinuity phenomenon occurs during normal phonation required experimental proof but it may have been inferred from the fact that most humans can reduce a musical tone in the larynx to a train of intermittent clicks as few as ten or less per second by strongly constricting the vocal chords and allowing the air to escape very slowly. During this type of phonation the breath is practically held. HUSSON has shown that although the volume of air expelled during each excursion of the vocal chords amounts to no more than 1 to 2 cm² the kinetic energy produced is very considerable. He gives the energy released per unit time as

$$e = \frac{1}{2} dm V^2 = \frac{1}{2} pPSV^3 dt$$

where dm is the mass expelled, p its volume density, P the pressure, S the surface of the glottic opening at the instant under consideration and V is the velocity of the air at the same instant. If V attains a figure of 200 m/s as for instance, in the singing voice, V³ will be in the order of 10¹² G.C.S. units. HUSSON (1963) has calculated that in the bat, in which the increment of air is only a few cubic millimetres but of which the velocity is a little less than 330 m/sec the energy is approximately 10⁹ G.C.S. units.

According to HUSSON most of the energy of the high-frequency components of the voice is absorbed by the walls of the supra-glottal air cavities by the formation of eddy currents and is used in impedance matching and other homeostatic functions. From the observed phenomena, HUSSON defines the role of the larynx during phonation as that of injecting large amounts of energy into the supra-glottal cavities. It will be seen that in principle the vibrations of vocal chords are very similar to the relaxation oscillations described by VAN DER POL.

In the toothed cetacean, full approximation of the arytenoids at the level of the thyro-arytenoid muscle is made impossible, partly because of the extensive attachment of these cartilages to the lateral wings of the cricoid, and partly because of their fusion to the cuneiforms which always

become approximated in advance of the arytenoids, thus preventing full approximation of the latter. Contraction of the thyro-arytenoid muscle, figs. 13 and 16 (MTA) draws the fused arytenoid and cuneiform cartilages (CAR, CUC) into the epiglottic trough (EPG) and intrudes the median epiglottic fold (EF) into the inter-arytenoid space. The anterior borders of the arytenoids then being locked in the epiglottic trough are prevented from moving laterally and contraction of the inter-arytenoideus muscle (MIA) brings about constriction of the rima glottidis. In this condition the whole epiglottis spout becomes divided into three narrow channels and below the level of base of the epiglottis, the laryngeal air sacs (CHM) become strongly compressed by the thyro-arytenoid muscles.

The whole action described above can be stimulated on the resected larynx of a dolphin by tightly encircling the epiglottic spout with the thumb and forefinger and by pressing together with the other hand, the arytenoid and thyroid cartilages. If air is then blown through the trachea the thyroid part of the larynx will expand to approximately twice its resting diameter due to inflation of the laryngeal air sacs, the wings of the thyroid cartilage being simultaneously pressed apart. If prevented from doing so by manual compression, the air escapes at the distal end of the spout in the form of three narrow jets. The median jet, being flanked by the stiff, cuneiform cartilages produces a high pitched whistle, whilst the two lateral jets, being surrounded by the more flaccid aryepiglottic folds, produce trains or bursts of staccato clicks. Both types of sound are composed of series of relaxations oscillations.

In principle, the mechanism of sound production is similar to that described by HUSSON for the vocal chords of Man except that the aryepiglottic folds are called into play instead of the thyro-arytenoid folds. This substitution, together with the involvement of accessory laryngeal air sacs is fairly common in terrestrial mammals (NEGUS, 1949). The main difference, of supreme importance, is the formation of a triple sound source due to the presence, unique among mammals, of a dividing septum in

the larynx.

When the epiglottic spout is opened by contraction of the cricoarytenoid and cricothyroid muscles, the anterior borders of the arytenoid and cuneiform cartilages are pulled out of the epiglottic trough and are thus free to separate. In these circumstances, contraction of the interarytenoid muscle pulls the anterior borders of the arytenoids and cuneiforms apart, the rima glottidis widens, and the whole epiglottic spout assumes a cylindrical shape of considerable diameter. This would be the normal condition during respiration, but an indefinite series of intermediate conditions could be assumed for the recirculation of air during phonation. It should be noted that if air is blown through the larynx without strong constriction of the epiglottic spout the organ tends to assume the cylindrical shape and no sound other than a hissing noise is produced. In the experiments described by EVANS and PRESCOTT (1962) there was no provision for laryngeal constriction and it must be concluded that such sound as was produced and measured must have been generated by the passage of air through the upper nasal plugs and valves so there is little wonder that the intensity field was asymmetrical.

During submergence, the blow-hole is closed, the thorax is collapsed and the bronchiolar sphincter muscles are presumably closed. In such conditions there would be positive pressure in the respiratory passages, and the laryngeal air sacs would be expanded within the walls of the thyroid cartilage. Contraction of the thyro-arytenoid muscles, figs. 13 and 16 (MTA) would act in compressing the air sacs on each side of the median fold and causing jets of air to be ejected from each aryepiglottic fold. If the interarytenoideus muscle were contracted whilst the thyro-arytenoid muscles were also contracted, constriction of the rima-glottidis would occur and a single jet of air would be ejected from the median aperture of the epiglottic spout.

Through the mechanisms described above it would appear that there are

arrangements for the production of either a double or a single jet of air. It may also occur that in some circumstances, a triple jet of air is produced. That these jets of air probably escape in the form of relaxation oscillations will be seen in considering the action of the nasopharynx.

THE FUNCTION OF THE NASOPHARYNX

Since the upper portion of the epiglottic spout is devoid of muscle, it is considered that constriction of the apex of the glottis takes place through the agency of the palatopharyngeal sphincter and the arcus palatinus. In view of the known mechanism for laryngeal constriction of Man, it would appear that some entirely new structure is being invoked for a part of this function in cetaceans. However, Man is the only mammal which does not possess a larynx which is normally intra-narial. During loud phonation in most mammals, the neck is stretched and the glottis disengaged from the posterior nares but in nearly all, there is a quieter (generally higher pitched) intra-narial phonation, during which this does not occur, the mouth is closed and the sound is emitted through the nostrils as for instance, in the nasal whining of the dog. The role of the arcus palatinus during this type of phonation seems to be quite unknown, but the mere tonus of the muscles must, to some degree, modify the operation of the intrinsic muscles of the larynx. For reasons concerned with monitoring already referred to in the text, it is believed that during submergence, phonation in cetaceans is entirely intra-narial. By strong constriction of the apex of the glottis by the palatopharyngeal sphincter and arcus palatinus, powerful resistance would be built up against the jets of air described in the last section until the air escaped as trains of relaxation oscillations. It is obvious that the recurrence frequency of such oscillations could be controlled over a wide range to produce high pitched, apparently pure tones, squawks, or staccato clicks. In every case the total wave form would not be sinusoidal, but very steep sided and the pulses would contain many harmonics of high intensity and frequency.

Tones produced when a stream of gas emerges from a jet are analogous to aeolian tones of which there are numerous examples such as the "singing" of telegraph wires, the "sighing" and "roaring" of wind in trees, the "whistling" of wind in tall grass, etc., air emerging from a slit-jet tends to form alternately spaced vortices on each side of the air stream as is the case when wind passes a narrow obstacle. A photograph (by the Schlieren method) of a high-velocity jet of air from a circular opening is shown in fig. 19 where it is clearly seen that the emergent jet is divided into sections of nearly equal length. KRUGER and SCHMIDTKE (1919) have shown that the frequency of the tones given out by air or other gases issuing from a small, circular jet conforms with the relation $N = kv/D$ where v is the velocity of the jet, D is the diameter of the opening, and k is a constant equal to 0.045 approximately for various mixtures of air, CO₂ and oxygen. Thus if, during each relaxation oscillation, the slits or jets at the apex of the epiglottic spout vary in diameter between 1.0 and 0.1 mm as seems probable from observation of resected larynges, and the velocity of the jets reaches 0.333×10^5 cm/sec, i.e. slightly above the speed of sound (HUSSON loc.cit), each pulse will contain frequencies between 15 and 150 kHz. This calculation is in good agreement with the frequency analyses of the echolocating pulse of Tursiops made by KELLOGG (1961). With greater jet diameters and greater jet velocities the frequency spectrum will exceed these limits. Such frequency spectra are commonly referred to as "white noise" but the wave form of a fraction of a pulse may be revealed by the oscilloscope as shown in fig. 8.

If air-jet pulses fall on the open mouth of a cylindrical pipe "oscillator", resonance is set up at the correct distance and the pipe emits powerful ultrasonic vibrations as high as 100,000 p.p.s. Even at the highest frequencies the relation $\lambda/4 = l + 0.6 R$ is valid for a closed pipe where l is the length of the pipe and R its radius. Since the only closed pipes in the vicinity of the glottis of a cetacean are those provided by the

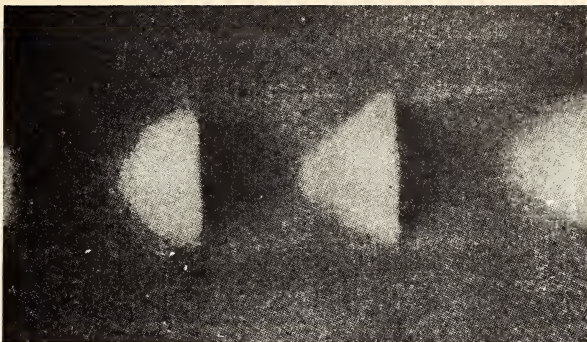


Fig. 19 : Schlieren photograph showing structure of jet of Hartmann and Troles' Air-Jet Generator
(By courtesy of G. Bell and Sons).



Fig. 20 : Vortex streets formed by a jet of air striking a sharp-edged wedge.

posterior nares of which the values l and R are relatively very large resonance phenomena could only occur in the low frequency sonic, range i.e. at about 1 kHz. Such resonant cavities would be quite unsuitable as sources of sound, as the mechanical coupling between the air contained in the nares and the animal tissues it would be very weak. In considering the use of resonators in conjunction with maintained sources of sound it is important to bear in mind that the action of a resonator is not to magnify the sound after it has been produced by the source but to enable the latter to develop a greater output.

Edge-tones arise when a jet of air strikes a more or less sharp edged wedge (see fig. 20). A tone first occurs when the "edge" is at certain minimum distance from the jet, this critical distance between dependent on the velocity of the gas issuing from the jet. BROWN (1937) found four different stages of stable vortex formation within the sound sensitive range of a jet. In this range the frequency N varied with h , the distance of the wedge (20°) and the mean velocity u , in accordance with the relation $N = 0.466 c (u-40) (1/h-0.07)$ where $c = 1, 2.3, 3.8$ and 5.4 for the four stages respectively.

It is tempting to think of the ventral surface of the vomer of cetaceans as constituting an "edge" in the path of a jet of air issuing from the apex of the glottis but its ventral surface is not particularly sharp and the mean values of u and h in the above equation are such as to produce frequencies only in the sonic range 1-10 kHz. Here again the mechanical coupling between the edge-tone vibrations and the sea water would be very weak.

If the sound source for echolocation in the cetaceans is produced by high-velocity air jets at the apex of the glottis as postulated, how then, are these vibrations transmitted to the bones of the rostrum and thence to the sea water with minimum loss of energy?

As previously stated, the ventral and lateral aspects of the aryepiglottic folds at the apex of the glottis lie in a deep recess, figs. 14, 17 (SRC)

in the palatopharyngeal sphincter, and the dorsal surface of the fused arytenoid and cuneiform cartilages make contact with the superior constrictor muscle (MSC) which is attached to the sphenoid bone at the base of the skull. The sphenoid bone is fused to the mesethmoid and vomer. The direction of the openings of the mucous ducts (MD) on the posterodorsal aspects of the palatopharyngeus muscles is such that if the palatopharyngeal sphincter were contracted, the recess (SRC) would normally be full of mucous and consequently the apex of the glottis would be acoustically coupled to the surrounding structures. Any vibration of the cartilages and folds would therefore be transmitted to these structures with very little loss of energy.

It is well known that cavitation, with the formation of gas bubbles, occurs when solid surfaces, immersed in liquids, vibrate with sufficiently high velocity. If the liquid contains dissolved gas, this will come out of solution when the total negative pressure at the vibrating surface in contact with the liquid falls below the saturation pressure of the gas in the liquid. Since there would normally be a great deal of dissolved gas in the mucous coating of the posterior nares after surface breathing, cavitation at the palatopharyngeal sphincter would be almost bound to occur. The presence of gas bubbles, if allowed to remain at the sphincter, would seriously interfere with the transmission of sound. It would, therefore, appear to be essential that some mechanism be provided for the elimination of bubbles at this point. It is for this reason that I believe that a copious flow of degassed mucous is poured over the sphincter from the mucous ducts which are so numerous and evenly distributed. It may be that this is also the reason for the heavy mucous lubrication of the vocal structures in other mammals.

Since the pressure on the laryngeal air sacs could be presumed to be symmetrical about the medial septum, the two trains of oscillations from each aryepiglottic fold would be identical in phase and frequency.

Decussation of the muscles of the palatopharyngeal sphincter on each side, with those of the other, would provide for the phenomenon of synchronisation, described in VAN DER POL's third property of relaxation oscillations. The fourth property of relaxation oscillations would ensure that the two lateral trains of vibrations were equal in amplitude. In the formula $T_{rel} = K r/s$ the value r can be regarded as being equivalent to the force exerted by the palatopharyngeal sphincter, and the value s , equivalent to the difference between the inherent elasticity of the cartilages and muscles, and that of the air in the larynx. Since the value s is a constant, the period T_{rel} could be directly controlled by regulation of the palato-pharyngeal sphincter. A steady pressure could be maintained on each side of the larynx by simultaneous contraction of the two air sac systems, through the operation of the thyroarytenoid muscles.

If the transmission of sound energy from the apex of the glottis (assuming the latter to be acoustically coupled to the surrounding structures in the manner described above) is considered in conjunction with the distribution of air spaces it is not difficult to see why the maximum energy is found along the central axis of the rostrum.

As they ascend the posterior nares, the two palatopharyngeal muscle masses are enveloped ventrally and laterally by extensions of the pterygoid air sinuses, figs. 14, 17, 18 (PTS), and dorsally by the lumen of the nares themselves. Any sound energy imparted to the two muscles by the two sides of the apex of the glottis would undergo total reflection at the air interface and could therefore only travel anterodorsally along the muscle fibres towards their insertion on the posterior aspects of the palatine and maxillary bone; fig. 18 (PAL, MX). Here the acoustic coupling must be very nearly perfect since the facial extensions of the muscle fibres and sheath enter the matrix of the bone and follow the anteroposterior orientation of the trabeculae in the form of long, dendritic processes. The excellence of this

coupling can be demonstrated by the use of acoustic probes in the manner described by FRASER and PURVES (1960) and PURVES and VAN UTRECHT (1963). The sound energy of the larynx is thereby distributed to the bones of the rostrum as a double source.

Assuming the thyro-arytenoid muscles to remain contracted, a single jet of air could be induced by contraction of the interarytenoid muscle figs. 13 and 16 (MIA). Such an air jet would escape as a train of relaxation oscillations through the minute aperture between the cuneiform cartilages make contact with the roof of the nasopharynx, fig. 14, vibrations initiated in the cuneiforms would be transmitted to the base of the skull in the interval between the two air-sac systems, fig. 18, as a single train of relaxation oscillations. From this point they would be transmitted to the mesethmoid and vomer as a single source. The arrangement described above provides for either a double or a single source or both simultaneously. One of the most important theorems applicable to sound waves is HUYGHEN'S Principle of Superposition. On this principle the resultant displacement of a particle of the medium through which two or more trains of waves are passing is obtained by the vector addition of the separate displacements due to each wave-train independently. This principle is also applicable to velocities and accelerations but not to the squares of these quantities. Thus, two periodic vibrations of the same frequency, of amplitudes a and b and phase difference e , combine to form a periodic vibration of amplitude $(a^2 + b^2 + 2ab \cos e)^{\frac{1}{2}}$. If the amplitudes are equal ($a = b$) and the phases are the same $e = 0$ superposition gives a vibration of double amplitude $2a$; but if the phases are opposed $e = 180^\circ$ the resultant amplitude is zero. In the more general case, the amplitude may vary between $(a + b)$ and $(a - b)$ according to the phase difference e . Such superposition of vibrations is more commonly referred to as interference. In the cetacean, the bony rostrum remains divided into three sections throughout life since the two maxillary bones never fuse at the intermaxillary suture and the vomer, although fused at its proximal end to the base of the skull, lies in a channel formed by the mesial borders of the maxillary bones but never unites.

with them. In this respect the Cetacea are unique among the Mammalia. However, as there is no air cavity separating the bones, sound can be conducted from one side of the rostrum to the other, though somewhat imperfectly, due to the lower acoustic impedance of the cartilage of the vomer.

If as postulated, the two sides of the base of the rostrum constitute a double source of identical phase and frequency, the sound intensity in the sagittal plane of the head will always be at a maximum, since all the disturbances from the various elementary areas constituting the two sound sources will arrive at this plane in the same phase. If the vomer is also conducting sound, the effect will be greatly enhanced. Outside the limits of the skull the two sound fields overlap, the phenomenon of interference will occur, so that in directions inclined to the sagittal plane the intensity will be less, diminishing steadily to zero when the difference in distance between the nearest and farthest elements of the double source is rather more than half a wavelength. In a direction still more inclined the sound will increase again to an intensity 0.017 of that on the sagittal plane, passing through successive zero and diminishing maxima values as the inclination increases. The angle θ at which the first silence would occur, i.e. the semi-angle which would delimit the primary beam would be $\sin^{-1}(0.61\lambda/R.)$. Thus the primary or central beam would be confined to an area of small angle when the value $R.$, of the maximum distance between the sound sources was large compared with wavelength λ , of the sound emitted, i.e. the directionality would be sharp when the frequency was high. The polar distribution of amplitude and intensity after STENZEL (1927) is shown in fig. 21. The interference between two independent trains of high-frequency waves in water has been demonstrated by BOYLE et al (1926). They mounted two piezo-electric quartz transmitters vibrating with the same frequency (96 kHz) and amplitude side by side in a tank of water in such a way that their primary beams overlapped. Fine coke dust sprinkled in the water settled in the nodal planes, and was ultimately caught on a whitened

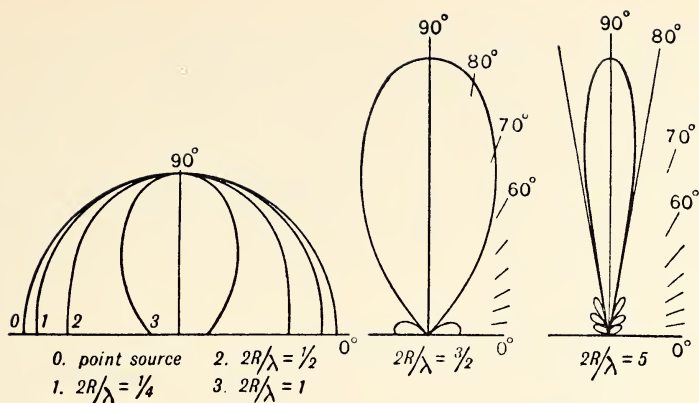


Fig. 21 : Polar diagrams showing variation in sound fields at various frequencies (after Stenzel).



(b) Frequency, 178,000 p.p.s.

$$\frac{\lambda}{D} = 0.055$$

Frequency, 129,000 p.p.s.

$$\frac{\lambda}{D} = 0.076$$

Fig. 22 (a)

Fig. 22 (b)

Fig. 22 (c)

- Supersonic Beams of Sound - Showing Primary and Secondaries

(Dr. R.W. Boyle)

surface below the sound beam. Fig. 22a shows how the distribution of particles resembles the orientation of the trabeculae of the bone in the rostrum of a cetacean. These authors have made visible by the same technique, the high frequency beams from a large quartz transmitter, fig. 22b, c. Using a transmitter 15.3 cm diameter at a frequency of 135 kHz, the wave length in water therefore being 1.11 cm they found that the semi-angle θ , of the primary beam was approximately 5° , which agrees with the theoretical relation $= \sin^{-1} 0.61 \lambda/R$ given above.

THE FUNCTION OF THE SKULL AS A TRANSDUCER

In the previous section it was shown, from anatomical and theoretical considerations why sound generated in the larynx should be concentrated along the sagittal plane of the head. Tables I to IV however, show that there is a further concentration of energy at the anterior extremity of the rostrum. Table IV of sound intensity measurement taken inside the mouth on the hard palate are particularly noteworthy since they show that the component bones of the rostrum tend to act as transducers concentrating energy in the anterior direction. Sound levels in db. taken in the mid-line 4 cm anterior to the first tooth, with the needle penetrating the vomer and its cartilage, are rather more than three times those taken at the same level on the maxilla. Both sets of readings increase in value towards the anterior extremity of the bone and then show a sharp drop in the soft tissue at the tip of the snout. This final drop in intensity was probably due to some form of discontinuity such as decomposition, involving the presence of gas bubbles.

From the level of the first tooth to the anterior extremity of the rostrum there is an increase in intensity in the maxilla of 21 db and in the vomer of 24 db. This concentration anteriorly is mainly due to the general shape of the bones of the rostrum but is probably greatly assisted by the orientation of the bony trabeculae. The vomer and its cartilage takes the form of a long, tapering rod decreasing in diameter from about 2 cm to a few mm with the trabeculae of the bone orientated antero-posteriorly

in conformity with the shape of the rod. It has been suggested (not published) that the cartilage of the vomer constitutes the main transducer in the cetacean skull - transmitting longitudinal vibrations to the tip of the snout. Evidence in support of this idea is provided in the Common Dolphin Delphinus delphis by the presence of longitudinal extensions of the pterygoid air sac system on each side of the vomer on the ventral aspect of the maxillary bones. It should be borne in mind, however, that such longitudinal vibrations as are transmitted by the vomer would have directional properties only within the confines of the skull. The diameter of tip of the vomer is so small that it would act as a point source for the whole frequency spectrum of sounds known to be emitted by cetaceans. The resultant sound field in the ambient water would be spherical and therefore non-directional. It is conceivable that this property is made use of in long range-echolocation. This idea is inconsistent with the experimental results of NORRIS et al. (1961) who found that blindfold captive specimens of Tursiops were unable to locate food fragments placed below the level of the chin (fig. 23). In a spherical sound field radiated from the tip of the snout, echoes of equal intensity would be received from food fragments placed above or below the level of the chin. NORRIS at first attributed this phenomenon to an incapacity of the dolphin to hear echoes below the level of the chin but in a later, private communication he stated that the animals could hear well through the lower jaw. From these observations it seems more likely that there is "blind spot" at this level from the point of view of phonation rather than of hearing.

It will be recalled that in the experiments described at the beginning of this paper I was unable to receive signal either from the lower jaw in the dead specimens or from below the lower jaw in the live specimens of Tursiops. If, as I postulate the source is located at the tip of the glottis and is transmitted through the palatopharyngeus muscles and vomer to the bones of the rostrum, the absence of appreciable signals from the

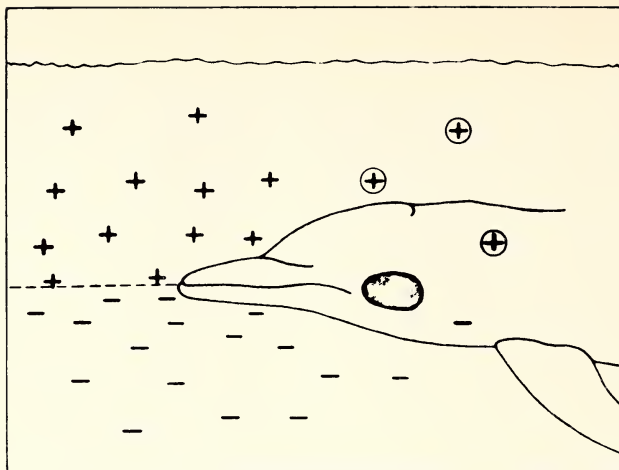


Fig. 23 : Diagram by Norris showing apparent limits of sonar detection of particles of food in a Bottle-nosed dolphin *Tursiops truncatus*.

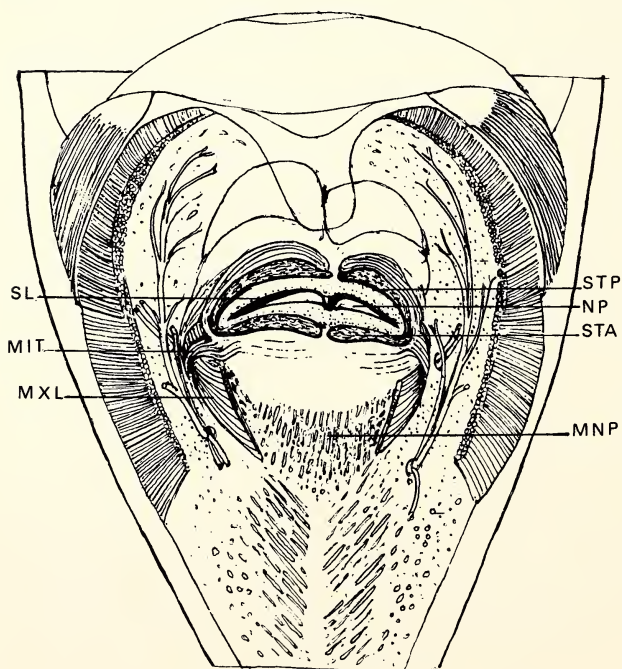


Fig. 24 : Diagram of a dissection of the dorsal aspect of the head of a Rough-toothed dolphin *Steno bredanensis* showing tubular air sacs.

lower jaws and chin can easily be explained by the presence of numerous acoustic discontinuities between these structures and the external surfaces. The lower jaw is for the most part acoustically isolated from the skull by the middle ear-sinus which surrounds the glenoid fossa. The apex of the glottis, fig. 14, is screened from the ventral aspect of the throat by the nasopharynx and pharynx, the palatopharygeus muscles by the pterygoid sinuses and pharynx, fig. 17, and the bones of the rostrum by the whole length of the oral cavity. Although the oral cavity and pharynx are not intrinsically air cavities in cetaceans as they are in terrestrial mammals it is certain that in common with the latter, the irregularities of the tongue and the mucous lining the whole oral tract will contain a high concentration of gas bubbles due to trapped air and the gaseous decomposition of food particles in the saliva and mucous. The presence of gas bubbles too small to be seen with the naked eye will cut down the sound transmission by as much as 80 % (PURVES loc.cit). Such acoustic discontinuities do not occur on the upper aspect of the rostrum except at the proximal end in the region of the supramaxillary air sacs. Although, owing to the high concentration of sound energy at the tip of the snout there would be a certain amount of spherical radiation in this region, it would be greatly reinforced by radiation from the dorsal aspect of the maxillae, so that echoes from above the level of the snout would always be dominant. If, as EVANS et al.(loc.cit) suggest, the frontal aspect of the skull acts as a parabolic reflector, most of this energy would be projected forward. It may be significant that in the body of the rostrum the bone trabeculae of the ventral half run horizontally parallel with the surface of the palate, but those in the upper half have an anterodorsal inclination.

In support of the theory of phonation propounded above it may be stated that if the sound produced by a small artificial whistle with relatively low air pressure in the larynx is distributed in the manner shown by Tables I to IV then a similar distribution of greater intensity would occur if any sound whatever were produced by the larynx of cetaceans.

THE ROLE OF THE UPPER NASAL PASSAGES IN PHONATION

In order that the larynx may function in the manner described in the preceding chapter, air must flow through the glottis into the upper bony nares. Moreover, since the animal is required to use its sonar system almost continuously whilst submerged at considerable depths and for long periods, this air must be conserved and recirculated for further use. Although it has not yet been proved it is my belief, from a study of the bronchiolar sphincter muscles in the smaller cetaceans, that prior to a period of moderately deep or lengthy submergence, the air is actively pumped out of the alveoli of the lungs into the upper bronchial passages and trachea. It has been stated that bronchiolar sphincter muscles do not occur in the larger Balaenopterid whales nor in the Bottlenose and Sperm whales Hyperoodon and Physeter. However, as SCHOLANDER (1940) has suggested, these larger whales probably pass straight through the "danger zone" to depths at which alveolar collapse occurs through hydrostatic pressure alone, thus avoiding nitrogen absorption.

Whatever the method of alveolar collapse, it is likely that during prolonged submergence, the thorax is immobilized and takes no part in phonation in cetaceans as it does in terrestrial mammals. It is possible that cetaceans have to "make do" in phonation with the amount of air that can be contained in laryngeal air chambers. It can be demonstrated that the large laryngeal air sac of the balaenopterid whales, completely fills the lumen of the trachea when inflated and is structurally homologous with the laryngeal air sacs of the odontocetes.

Although the amount of air used in a burst of sonar activity is probably not known it is possible to estimate in broad terms, the amount that would be used if phonation occurred by the method described in the preceding chapter.

Experimentally, a resected larynx of Tursiops truncatus used approximately 120 cc of air in the artificial production of a train of relaxation oscillations lasting 10 seconds with an average pressure of 25 mm Hg. This is probably

an overestimation of the amount used in life and it is interesting that the theoretical estimate is about half this quantity.

Fig. 7 shows a series of three pulses with the oscilloscope set at 100 cycles per sec. The recurrence frequency is therefore 300 pps. As the camera exposure was 0.04 sec there are 4 to 5 clicks superimposed on each pulse and the duration of a single click is approximately 0.2 m/sec. Taking an average recurrence frequency of 150 pps during a 10 sec train of pulses and an average jet diameter of 0.05 the volume of air can be calculated if the velocity of the jet is known. The frequency content of the pulses, according to KRUGER and SCHMIDTKE (loc. cit.) indicates that the velocity is above the speed of sound but an estimate can arrive at in part with reference to Kinetic Theory. If the air in the respiratory tract of cetaceans reaches 300° C on the absolute thermodynamic scale and the difference in air pressure within the larynx is greater than that in supraglottal cavities by 1/3 atmosphere at any instant, then the difference in the kinetic energy of the molecules of air inside and outside larynx will be 48×10^4 dynes cm² approximately. This figure represents about the limit of the force than can be exerted by the thyroarytenoid muscle in Tursiops truncatus but a much smaller pressure difference could be assumed. The density difference, if the air were saturated with water vapour would be 3.5×10^{-4} gms per cc. If this pressure difference were released suddenly at the tip of the glottis then velocity of the escaping gas would approximate to the mean velocity of agitation of molecules of the gas along the axis of the glottis.

This is equal to $(P/p)^{\frac{1}{2}}$ where P is the pressure difference = 2/3 of the total kinetic energy and p = density difference = $((32 \times 10^4)/(3.5 \times 10^{-4}))^{\frac{1}{2}}$ = 30.2×10^3 cm sec. If the air is further accelerated by elastic recoil of the glottic cartilages to slightly above the speed of sound as HUSSON (loc.cit.) states, then the amount of air used during a burst of sonar lasting 10 secs with three laryngeal jets operating simultaneously with

0.2 m sec pulses at 150 per sec.

$$= 33.3 \times 10^3 \times \pi (0.025)^2 \times 150 \times 10 \times 3 \times 0.0002 = 60 \text{ ccs}$$

It should be pointed out that the above calculation is meant to apply to an animal of about the size of Tursiops but because pressures and densities are proportional, the jet velocity would be about the same for smaller values of P and p. The size-specific variables are considered to be intensity and recurrence frequency.

It has been postulated that the sound producing mechanism is located in the upper nares and is probably represented by the two valvular flaps which are to found on the lateral borders of the nasals plugs. LAWRENCE and SCHEVILL (loc. cit.) have described in great detail, the anatomy and major function of the upper narial structures in the delphinid nose but for the purpose of examining the hypothesis referred to above, it is necessary to describe some recent anatomical and experimental investigations on a specimen of Steno bredanensis.

It is proposed to use the same anatomical nomenclature, as assigned to the various structures by LAWRENCE and SCHEVILL but with different abbreviations. Fig. 24 shows the dorsal aspect of the head after removal of the integument and most of the musculature. The conspicuous features are the two pairs of tubular air sacs (STA, STP) which surround the lips of the blowhole. These are asymmetrical in size and orientation with the chord of the arcs lying at right angles to the nasal septum and mesethemoid. The lips of the blowhole are shown distended revealing the upper surfaces of the nasal plugs (NP), but when the sacs are inflated by air and drawn laterally by their intrinsic musculature (MIT) they approximate the lips of the blowhole. The posterior sac fits into a recess on the dorsal aspect of the nasal plug, fig. 17, and the anterior sac thrusts the anterior lip of the blowhole backwards into a recess above the posterior sac where the epithelium of the nares is sculptured to make a perfect fit. Thus the greater the pneumatic pressure in the tubular sacs the more perfect is the occlusion of the blowhole. Moreover, in this condition the posterior part of the nasal plug is prevented from moving upwards so that air injected

from below must pass into the premaxillary sac (SPM). In fig. 25 the thin, shield-shaped roof of the premaxillary sacs can be seen anterior to the blowhole; it should be noted that it lies approximately on the longitudinal axis of the head and has its own intrinsic musculature (MSM) which originates in the groove formed by the premaxillae (PRM). The cut surfaces of the proximal end pars profund (MXL) of the maxillolabialis can be seen. Some of the fibres of this muscle decussate over the premaxillary sacs and others enter the adipose tissue just above them so that contraction of the muscle compresses the sacs and draws the nasal plugs downwards. Since the origins of this part of the maxillolabialis on the posterolateral borders of the premaxillae also cover the connecting sacs (SCO figs. 24 and 25) contraction of the maxillolabialis also compresses the connecting sacs.

The connecting sacs are so-called because they connect the premaxillary sacs with the tubular sacs and it should be noted that in Steno the sac of the left side is very much reduced in volume and calibre compared with that on the right. By sealing the slots (SL) which lead from the upper nares into the posterior tubular sacs it is possible to inflate the tubular sacs with air through the connecting sac, by means of a hypodermic needle. It was found that the combined sacs took a little less than 10 ccs of air, and it is doubtful whether this figure could be more than doubled under pressure. As LAWRENCE and SCHEVILL have pointed out, manual pressure on the sacs in the living dolphin causes air to be extruded upward through the lips of the blowhole into the vestibular sacs (VS) fig. 26, which lie dorsolateral to the tubular sacs. This air escapes through the slots (SL) which lie above the level of the nasal plugs.

In fig. 27 the membranous roof of the premaxillary sacs has been cut away and the nasal plugs (NP) drawn posterodorsally out of the nares (N) to show their ventral surfaces. Two incisions have been made in the posterior tubular sacs and two probes (PR) inserted to demonstrate the connection between them and the premaxillary sacs (SPM). The flap-like lateral extensions of the nasal

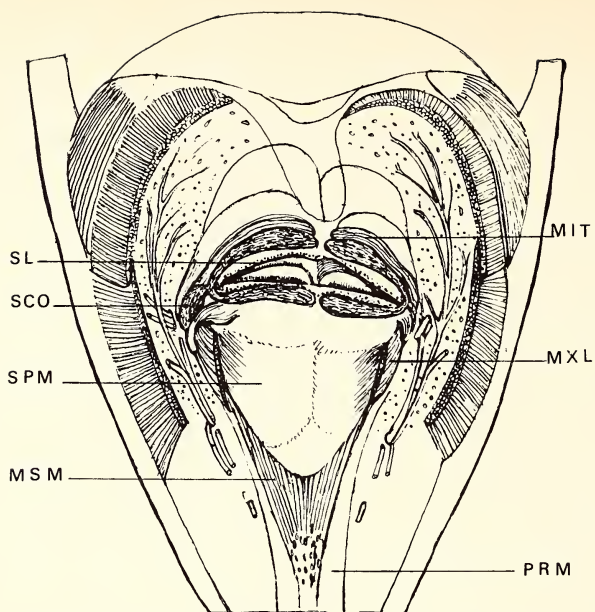


Fig. 25 : Diagram of a dissection of the dorsal aspect of the head of a Rough-toothed dolphin *Steno bredanensis* showing connecting and premaxillary sacs.

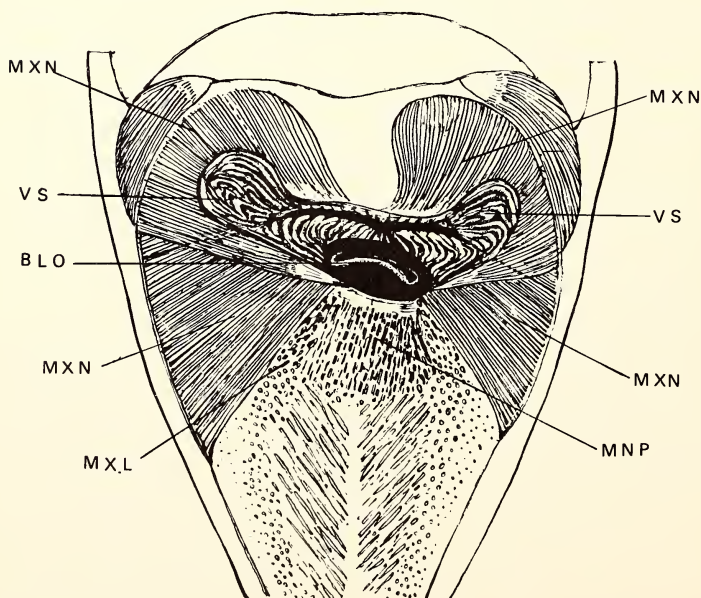


Fig. 26 : Diagram of a dissection of the dorsal aspect of the head of a Rough-toothed dolphin *Steno bredanensis* showing vestibular sacs.

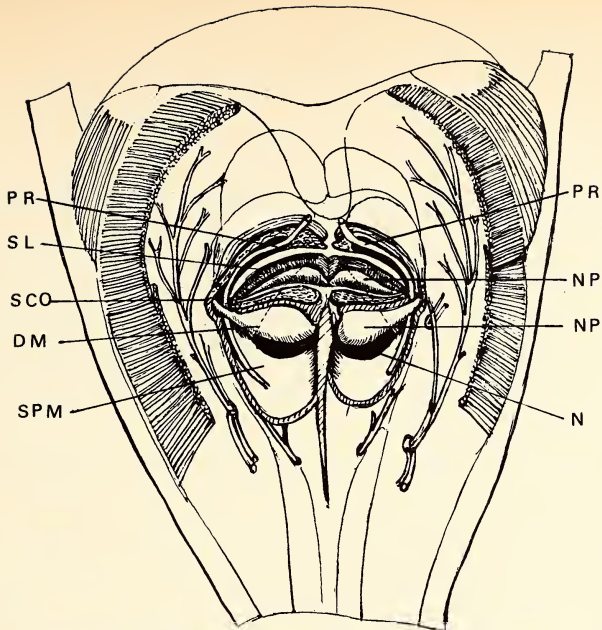


Fig. 27 : Diagram of a dissection of the dorsal aspect of the head of a Rough-toothed dolphin *Steno bredanensis* showing nasal plugs and lateral valves.

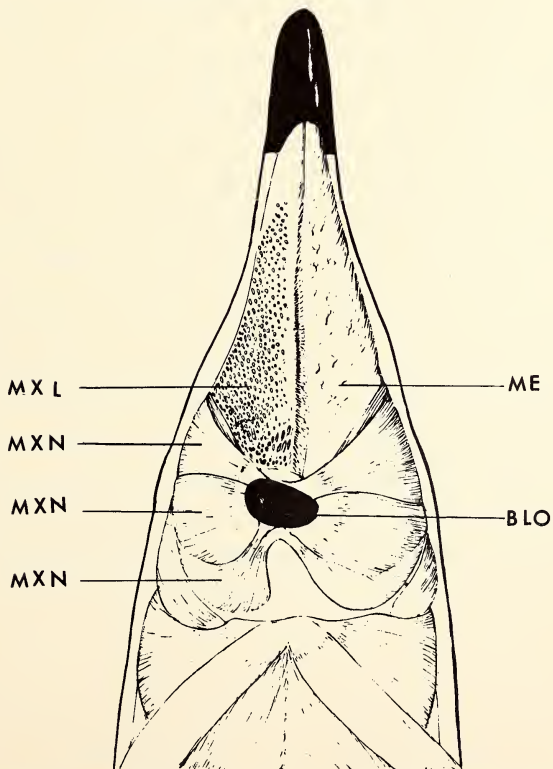


Fig. 28 : Diagram of a dissection of the dorsal aspect of the head of a Rough-toothed dolphin *Steno bredanensis* showing blowhole musculature.

plugs protrude into the connecting sacs (SCO) and are seen in front elevation in the diagram. It should be noted that they are concavo-convex with the concavity on the upper surface. The form is such that they act as unidirectional valves leading into the tubular sacs. Once the tubular sacs have been inflated fully, the air cannot escape back into the premaxillary sacs since the back-pressure seals the flaps on to the floor of the connecting sac and premaxillary bones.

Ventral to the nasal plugs are two diagonal membranes (DM dotted line) stretching from the lateral margins of the nares to the medial extremities of the slots (SL) leading into the posterior tubular air sacs. The mesial borders of these membranes are exceedingly thin and delicate and when air is blown up from below, the membranes fly against the ventral surfaces of the nasal plugs so that air can only flow between the former into the premaxillary sacs, thence to the tubular sacs. This arrangement ensures that unless the entire narial system is dilated by withdrawal of the nasal plugs from the nares by the nasal plug muscles, figs. 24 and 26 (MNP) and by contraction of the entire blowhole musculature, figs. 26 and 28 (MXN). See LAWRENCE and SCHEVILL (loc. cit.), such as occurs during respiration, any air pressure initiated from below at the level of the larynx will inflate the tubular sacs first. The upper blowhole having thus been properly occluded the premaxillary sacs will expand. The premaxillary air sacs in Steno are relatively small and contain a maximum of 50 cc of air when inflated. This probably represents the limit of the volume of air that can be used in a single burst of sonar. When the pars profundus of the maxillolabialis contracts, the connecting sacs are compressed, thus sealing off the entrance to the tubular sacs. The premaxillary sacs are also compressed and the contained air is driven back down the nares. It is possible that when the maxillolabialis is fully contracted, a slightly negative pressure can be produced in the superior nares by the action of the extrinsic muscles of the larynx and throat. The palatopharyngeal sphincter would meanwhile be slightly relaxed. The muscles of the throat of cetaceans are extremely

complex and a description of their function is beyond the scope of this paper.

It has already been stated that it would be possible to produce whistling noises by the passage of air through the valvular extensions of the nasal plugs, but because of the relatively large amount of air required for this purpose and the small capacity of the tubular sacs, such whistling would always be accompanied by loss of air into the vestibular sacs, thence to the water, if the duration of the whistle exceeded more than a second or two.

LAWRENCE and SCHEVILL have ascribed the function of a water-trap to the vestibular sacs (fig. 26) and there is no doubt that this is one of their main functions. A jet of water with a head of two atmospheres aimed directly at the blowhole of the head of Steno referred to above, caused the vestibular sacs to expand to their full capacity and then overflow but no water was observed to flow from the severed end of the trachea. Since many cetaceans have been observed to exhale before reaching the surface a water trap would appear to be essential. However, S. ANDERSON, Anton Brun Oceanographic Institute, Copenhagen, in a private communication stated that in Phocaena these sacs act as floatation devices when the animal is stationary or sleeping, ensuring that the blowhole remains clear of the surface when breathing. Recently dead animals have been observed to sink below the surface when the vestibular sacs have been punctured.

Both of these explanations of the function of the vestibular sacs raise the question of the asymmetry of the cetacean skull and upper nasal mechanisms. It has frequently been postulated that this asymmetry is associated with the sonar system although it is difficult to imagine from the physical standpoint what advantage could be gained from such asymmetry.

My view is that the total asymmetry of the cetacean skull and nasal system is associated with the mechanics of respiration, and the remarks of ANDERSON (loc. cit.) are relevant to one aspect of this function. The

cetacean "image" is that of a very active animal constantly moving through the ocean at high speed. It is well known, however, that like other mammals, whales and dolphins require rest and sleep and must seek relatively undisturbed surface conditions for this purpose. It would be of considerable disadvantage in these circumstances if the blowhole were placed centrally on the top of the head. According to LAWRENCE and SCHEVILL (loc. cit.) the average combined expiratory and inspiratory duration of the blow in Tursiops was 0.75 sec and was frequently accompanied by a certain amount of water spray.

In common with all mammals, the thoracic mechanism is such that inspiration is more rapid and positive than exhalation. If the blowhole were vertically orientated, a considerable quantity of the exhaled water spray and gas would be reinhaled on the inspiratory phase. This would obviously not occur in a dolphin in motion or in windy conditions.

If, during the course of evolution of the lateral displacement of the blowhole, the entire system of pneumatic cavities had remained symmetrical about the axis of the mesethmoid the former too, would have been moved laterally so that the head would then be hydrostatically unstable and there would be a constant tendency for the head to rotate until the blowhole was again top-dead-centre. It is clear that during the lateral displacement of the blowhole and nasal septum, the air sac system of the right hand side has become "parasitic" on that of the left, so that the whole system of air spaces remains approximately on the central axis of the skull and is therefore hydrostatically stable. The extreme example of this process is found in the Sperm whale Physeter catodon where the entire system of air sacs of the left hand side has disappeared, whereas that of the right is greatly hypertrophied and centrally disposed about the long axis of the head.

Although the plane of the mesethmoid makes an angle to the left of the sagittal plane, the long axes of the lateral diverticula of the nares, the

lips of the blowhole, and the chord of the crescent of the blowhole remain at right angles to the plane of the mesethmoid, so that the entire systems of the two sides have an anteroposterior displacement.

It follows that since the structures of the right side are larger than those on the left and are displaced anteroposteriorly, then the muscles which control these systems must also be larger and anteroposteriorly displaced. Finally the bones of skull which form the origins of these muscles must be commensurate with the soft parts so that the entire upper surface of the skull takes on an asymmetry that is subservient to the proper functioning of the soft parts.

In most odontocetes the left bony narial aperture is larger than the right and the naris follows a more vertical course. The epiglottic spout is bent slightly to the left (markedly so in the Ziphiidae and Physeteridae) and when the larynx is pushed upward into the nasopharynx the glottis moves towards the left posterior naris. The radiograph, fig. 29, shows the head of Steno in which a small strip of lead foil was placed across the chord of the curve of the blowhole with another bisecting the arc. It will be seen that the cross so formed, lies exactly over the left bony naris.

All this evidence suggests that in the Odontocete respiration takes place predominantly through the left naris. This is most obvious in the Physeridae in which the diameter of the bony aperture of left side is five to seven times greater than that of the right, and the nostril of the left side forms a continuous tube, the calibre of which is controlled by circular muscle throughout its length.

It is possible that the whole arrangement is conducive to more efficient external respiration, and in having greater survival value, is probably the result of natural selection. It can be demonstrated by a simple calculation that a pair of nostrils of equal calibre, such as is found in terrestrial mammals, is a relatively inefficient arrangement, as far as ventilation of the lungs is concerned. Consider two circular pipes of diameter 4 cm and 1 cm



Fig. 29 : Radiograph of the head of a Rough-toothed dolphin Steno bredanensis showing position of blowhole with respect to left narial passage.

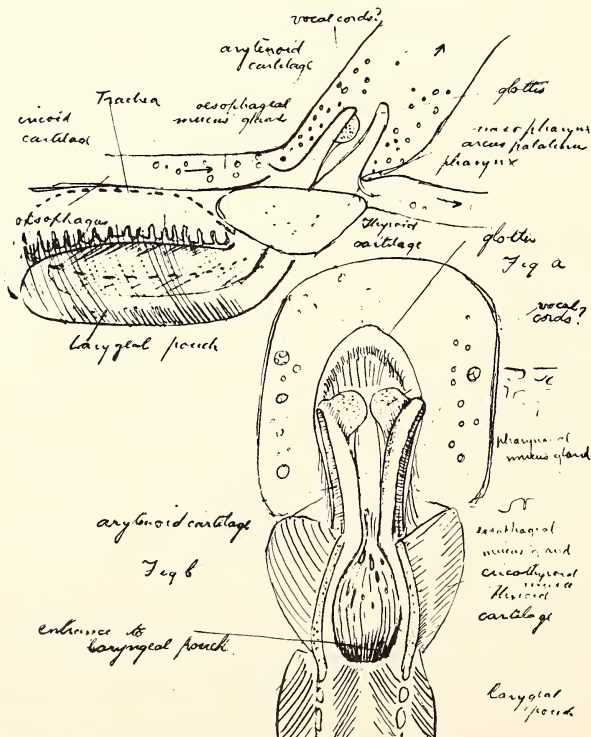


Fig. 30 : Sketch of the laryngeal sac in the Fin-whale Balaenoptera physalus. In fig. b the dorsal parts of the cricoid and trachea have been removed and the arytenoids rotated outwards.

length. Then the internal surface area is given by $2\pi R$ and the volume by πR^2 for each pipe. The ratio of total surface area to total volume for both pipes

$$= 2 (2\pi 2) : 2 (\pi 2^2)$$

The value π is a constant and can be neglected, therefore the ratio is

$$8 : 8$$

Suppose now that the diameter of one pipe is reduced to 2 cm and the other increased by a corresponding amount, becoming 6 cm, the ratio of total surface area to volume becomes

$$(2\pi 1) + (2\pi 3) : (\pi 1^2) + (\pi 3^2)$$

the ratio is

$$8 : 10$$

Thus at a given velocity, a greater volume of air could be passed through the two unequal apertures for the same surface area, as that for the two equally sized apertures. If passage through the smaller aperture were suppressed completely, the ratio would become

$$(2\pi 3) : (\pi 3^2)$$

$$= 6 : 9$$

In this case the surface to volume ratio is even more favourable, and the total volume of air passed through the single, larger aperture, is again greater than that through both of the original pair of 4 cm diameter. The greater one aperture becomes with respect to the other, the greater the advantage from the ventilation point of view, and it is my opinion that this principle is also involved in the asymmetry of the cetacean skull which finds its extreme expression in the *Sperm whale*. It is clear that in this Super-family the smaller aperture plays no part in external respiration.

CONCLUSION

In commencing this discussion, I stated that the arrangement of paired nostrils of equal diameter was an inefficient mechanism, from the point of

view of breathing. Why then is it present in all terrestrial vertebrates and in most fish? It is my opinion that the explanation is to be found within the cognisance of the whole purpose of bilateral symmetry in living organisms. Efficient motion in a chosen direction, became possible in evolutionary history, only when sensory and locomotory organs of various kinds became symmetrically disposed about a central axis of the body. By such an arrangement, animals became able to detect differences between the environment on the two sides of the body, and to move towards a preferred environment without experimentation.

It is this general principle, which I believe to be embodied in the possession by all active vertebrates of paired nostrils, and of the forked tongue in certain reptiles. The nostrils are the seat of the olfactory conchae and are, therefore, primarily sensory organs. Just as it is necessary to have two ears for directional hearing, so it is necessary to have two nostrils for the purpose of directional olfaction. Modern man has become to be almost totally independent of the directional properties of his sense organs and tends to neglect the importance of this aspect of their physiology when studying the lower vertebrates. At first sight it may seem that the nostrils are not sufficiently widely separated to form a time or intensity base for directional olfaction. However, the planes of the nostrils in most animals lie across widely divergent axes, and air is inhaled and exhaled from a considerable distance along these axes, as may deduced from simple laboratory experiments and by the observation of the columns of the water vapour expelled from the nostrils of animals in cold temperatures. Most animals are able to follow with great accuracy an invisible, undulating scent-trail on the ground. As an example, if the leg of a frog be trailed in a winding course across a piece of white card and the card be allowed to dry, there remains no visible trace of the track of the foot. Nevertheless, a grass-snake can follow this trail with perfect accuracy. It is possible that this is achieved through the detection by the organs of

JACOBSON, of slight differences in the scent on the two prongs of the forked tongue. If a dog were forced to experiment by quartering the ground every time a scent changed direction, a great deal of time and muscular effort would be required - in other words, the system would be inefficient. It is conceivable that when an animal "sniffs the wind" away from the ground, the nostrils are used in conjunction with the extremely sensitive, tactile vibrissae, which lie in regularly spaced rows on either side of the nose and probably act as wind direction indicators. The idea that these are used solely for measuring the distance apart of obstacles, is, in my opinion, erroneous.

Olfactory organs are absent in odontocete cetaceans and the blowhole is entirely subservient to breathing; thus there is no need for paired nostrils. The blowhole is, therefore, adapted for more efficient ventilation. For two examples in the Vertebrata which "prove the rule" one may draw attention to the organisation of the olfactory organs in a group of Devonian fishes, the cephalaspids which led a completely sedentary life on the bottom of the sea. In these fish, there is but one nostril, mesially placed, but there is clear evidence internally, that at some time in their evolutionary history, they possessed two external nostrils.

The other example is in the paired nostrils of the Mysticeti, the baleen whales, which possess both olfactory conchae and olfactory lobes in the brain. The fact that the latter two structures are relatively small, and that the animals live permanently in the sea has led to the supposition, by some cetologists, that the sense of smell is either reduced or absent in the Mysticeti also. However, the olfactory organs are in absolute terms much larger than in most other mammals and it is difficult to see why they should be commensurate with the total size of the animal. When it is remembered that the Mysticeti are plankton feeders, and that plankton-rich, sea water frequently has a distinctive odour, it is not difficult to imagine that these large animals may "sniff the wind" in search of their food.

It is doubtful, however, whether there is any intranasal directionality in the olfactory sense and it is possible that the tactile vibrissae on the surface of the head can act as long-range, wind direction receptors as well as underwater close-range receptors.

Perhaps the most striking evidence in favour of the hypothesis of a laryngeal source of phonation in cetaceans is that afforded by the Mysticeti. SCHEVILL et al. (1964), who first established that the persistent 20 Hz sounds recorded in certain parts of the Atlantic were those emitted by the Fin whale Balaenoptera physalus, has compiled a list of those mysticetes known to emit sounds, together with the authorship of the observations. More recently, PERKINS (1966) published sonagrams demonstrating that Fin whales were also capable of emitting whistles and chirps with frequencies up to 5 kHz. SCHEVILL (1964) drew attention to the laryngeal sac in the Mysticeti and indicated its possible use in phonation. Since most of the published work on the larynx of Mysticetes concerns foetal and juvenile specimens it might be worthwhile drawing attention to a few details concerning the sub-adult larynx which do not seem to have been described. In 1955 I had the opportunity to examine the larynges of 18 Fin whales at Steinshamn, Norway, and two of these were taken to the British Museum (Natural History) for dissection and exhibition. Since they differ in some important respects (which are relevant to the subject of phonation) from those described in the literature I propose to publish a more detailed account at some future date. A sketch from my log-book is reproduced in fig. 30. In all the specimens examined by me there was a semidiscoid flange projecting forward from the apex of each arytenoid cartilage. The flange was about 8 cm in radius and about one centimetre thick. In the more adult specimens the mesial surface was covered with closely-packed, warty rugosities of approximately one millimeter diameter so that the whole surface presented an appearance similar to that of the tongue in terrestrial mammals. Microscopic examination revealed a thick, cornified epithelium with a very deeply papillated zona germinativa like that of the external skin, and it is clear that these surfaces were subject to considerable wear. When the

arytenoid and epiglottic cartilages were approximated and laterally compressed as if by the arcus palatinus, the mesial surfaces of each flange became closely opposed and the anteroventral borders of the double assembly fitted deeply into the trough formed by the epiglottis. The flanges themselves were composed entirely of elastic tissue and it is certain that if air were blown through the glottis from below with sufficient pressure it would cause the system to vibrate harmonically and probably with a fixed frequency, whether the larynx was used for phonation or not. In the more juvenile specimens, the flanges were smaller and their mesial surfaces smoother although incipient rugosities were present. It is possible that the formation of the rugosities was correlated with the onset of sexual maturity. The origin of these arytenoid flanges is not difficult to find when the foetal specimen is examined. The "arytenoid body" as described by CARTE and MACALISTER (1868), SCHULTE (1916) is wholly semidisoid in shape and consists of a very small posterior arytenoid cartilage and a large anteriorly directed membrane which is homologous with the phonatory "arytenoid fold" of the ungulate mammals. During the postnatal lengthening of the arytenoid cartilage and the epiglottis, this membrane is carried dorsally so that it becomes remote from the main body of the larynx. Its functionality in the adult is indicated by its isogonic growth in diameter and thickness, and its situation at the apex of the glottis gives support to the notion that the phonatory region of the larynx, is, as in the Odontocete, at the tip of the epiglottic spout. In a female 17.75 m long, the laryngeal pouch was 120 cms in length, 40 cms in depth and 30 cm wide. When the animal was lying on its back the whole sac fitted neatly into the lumen of the trachea, in this part of which the cartilaginous rings were fused into a solid plate dorsally and absent ventrally. The great mass of the thyroarytenoid muscle, which formed the ventral and lateral walls of the sac was 20 cm thick at its greatest width. The muscles of this system have been adequately described by HOSOKAWA (loc. cit.) and it is apparent that the sac and its muscle system is homologous

with the laryngeal air sacs and their closing muscles in the Odontocete. It is clear from the unique construction of the trachea and the muscular arrangement, that the sac can be drawn up into the lumen of the trachea so that it isolates the supraglottal air spaces from the thorax. It can be conceived that an arrangement such as this could be used to evacuate the lungs if this did not occur through hydrostatic pressure at moderate depths. Since there are apparently no distensible air sacs in the superior nares phonation by the larynx would require more pressure than in the Odontocete but the muscles of the laryngeal sac seem quite adequate to perform this function and to produce the large energy outputs which have been measured.

In the Mysticeti, as in the Odontoceti, the larynx is coupled anatomically to the bones of the rostrum by the palatopharyngeal muscle complex, and it is conceivable that it is so-coupled acoustically. It is significant that in common with smaller cetaceans, the component bones of the two sides of the rostrum remain separated from each other by the vomer throughout life. The length of a 20 Hz sound-wave in water is 70 metres approximately, therefore very little directionality could be imparted to the 20 Hz pulse by the "double-source" arrangement, as described for the Odontocete. However, the wave length of the 5000 Hz "chirp" described by PERKINS (loc. cit.) is only 30 cm. The width of the skull in an adult Fin whale can be in excess of five times this figure, therefore the chirp must have very definite directional properties, if propagated by the skull.

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ABSTRACT

A great deal of speculation has arisen about the mechanism of phonation in cetaceans and a number of different hypotheses have appeared in the literature. Some authors locate the sound producing mechanism among the various pneumatic chambers which are to be found in the upper part of the blow-hole, but others believe the sound source to be laryngeal.

Experimental results obtained by locating a sound source in the larynx of fresh, dead cetaceans and by measuring the sound intensity at various points on the surface of the head have shown that the greatest energy is always distributed along the central axis of the skull notably along the vomer and particularly at the tip of the snout. These results were strikingly similar to those obtained by measuring the near-field distribution of sound emitted by live dolphins at Communications Research Institute, Miami, thus indicating that the sound source is probably laryngeal in the living animal.

A study of the larynx, palatopharyngeous muscles, basicranial air sinuses and the bones of the skull indicate that the larynx acts as a triple source to produce through interference phenomena, highly directional sound beams in the near-field.

A study of the upper narial mechanism shows that the accessory pneumatic air chambers are necessary for recirculation of air and occlusion of the blow-hole during phonation but are not directly involved in echo-location.

II

Discrimination et identification
par les sonars des animaux

Discrimination et identification
by the animal's sonar

DISCRIMINATIVE ECHOLOCATION BY BATS

by

Donald R. GRIFFIN

The active sonar or echolocation of bats has become better and better understood through a series of discoveries, each of which seemed so incredible when first considered as a hypothetical possibility that biologists were reluctant even to ask the pertinent questions. Spallanzani and Jurine demonstrated in the 1790's that bats could be disoriented by covering their ears, but the climate of scientific opinion was unprepared to consider that animals might generate sounds inaudible to human ears, still less that echoes of such sounds could serve to orient rapid and agile flight. (For historical reviews see Galambos, 1942; Dijkgraaf, 1946, 1960; Griffin, 1958 - Chapter 3; or Vincent, 1963). Barely had we accepted the fact that bats could locate stationary objects by echo when behavioral observations suggested that even small insects might also be intercepted by active sonar (Griffin, 1953). Only some years later did differential masking experiments with low and high frequency noise demonstrate conclusively that small insects could be captured by echolocation at rates of several per minute (Griffin, Webster, and Michael, 1960).

In what might be called a state of dynamic habituation to successive surprises, we have inquired in recent years how well bats can distinguish between echoes and other sounds, or between the echoes from different objects. Contrary to hopeful expectations when this conference was arranged, I have no new data to present, and the following speculations are based primarily on three recent papers on bats' resistance to jamming

(Griffin, McCue and Grinnell, 1963), on fish catching by echolocation (Suthers, 1965), and on discrimination between similar targets (Griffin Friend, and Webster, 1965). My objective is to stimulate constructive discussion and informative investigations in the future.

Insectivorous bats belonging to several families of the suborder Microchiroptera appear to be very efficient in catching flying insects, although only Gould's studies of two genera of the family Vespertilionidae (1955, 1959) provide semi-quantitative data from natural conditions. Other insectivorous families such as the Emballonuridae and Rhinolophidae employ different types of orientation sounds, and their interception strategies deserve thorough analysis, perhaps by methods such as those already developed by Webster (1963). It would be especially desirable to learn just how these bats catch insects under natural conditions as well as in captivity. Bats of the families Vespertilionidae and Molossidae usually employ frequency modulated pulses with an octave of frequency sweep during one or a very few milliseconds. The Rhinolophidae use constant frequency pulses, with a brief but variable interval of falling frequency at the end and sometimes a rising frequency at the start (Griffin, 1962). The Emballonuridae are less specialized for echolocation and seem to have better vision, but even when hunting insects in the daytime, as Saccopteryx does routinely, they resemble other predatory bats in accelerating the pulse repetition rate at each catching maneuver. The frequency patterns in Emballonurid orientation sounds are less easily characterized, but multiple harmonics are usually present and durations vary from one millisecond or less to some pulses that rival in duration those of the

Rhinolophidae. Another important group of neotropical insectivorous bats is the subfamily Chilonycterinae of the family Phyllostomidae. Their sonar signals are somewhat like those of the Emballonuridae, but virtually nothing is known about their insect-catching tactics under natural conditions.

If close analysis should show no differences in the way these orientation sounds are used, this would suggest that pulse frequency pattern is not important or that bat brains can be adapted to recognize echoes regardless of such patterns, provided only that the pattern used by a particular species is one to which its auditory brain is also adjusted. On the other hand, sufficiently penetrating investigation might reveal significant differences in what these various groups of bats actually learn from their variously structured echoes, and such findings in turn would suggest interesting correlations between structure and function of the probes of sound bats use to keep in touch with their surroundings.

Even the best-studied species of the family Vespertilionidae present us with unexplained variations in pulse structure. Both Eptesicus fuscus and Lasiurus borealis emit pulses that vary considerably in duration and in rate of frequency sweep. As with all other bats yet studied, difficult maneuvers and demanding situations elicit shortened pulses of the "chirp" or frequency modulated pattern. But when flying at moderate altitudes in relatively straight lines, longer pulses often show considerable periods with a nearly constant, or slowly changing frequency. Is different

information being extracted from the environment by these different types of orientation sounds? The Doppler effect and frequency differences between outgoing pulse and returning echo seem unlikely to be of crucial importance, because these bats almost always avoid overlap between pulse and echo (Cahlander, McCue and Webster, 1964; Webster, 1963). The Chilonycterine bats studied by Novick (1965), together with the Rhinolophidae discussed by Moehres (1953) differ from the Vespertilionidae in using sufficiently long pulses to assure pulse-echo overlap under many conditions including insect capture. Surely these differences in acoustical design must be related to differences in behavioral tactics, but we will remain ignorant about such matters until direct and detailed descriptive and experimental studies of insect hunting are carried out. These will be most useful if the relative positions of bat and insect are measured with reasonable accuracy throughout entire sequences of search, approach, and interception. Of course the orientation sounds must be simultaneously recorded sufficiently well to show not only pulse duration, pulse to pulse interval, and frequency pattern, but ideally the emitted intensity as well. The photographic triangulation employed by Griffin, Webster, and Michael (1960) is a first step in this direction, but considerable improvement in detailed accuracy would be possible and highly desirable.

One procedure often suggested by physical scientists is multichannel recording from several microphones at pre-arranged locations, followed by a comparative analysis of the time relations between the emitted pulses.

In theory this can determine the bat's position with considerable accuracy, but preliminary attempts have so far been frustrated by such practical problems as the 10 to 30 db variation in sound intensity emitted in various directions and the consequent difficulty in making accurate comparisons of pulse onset, for example, at microphones ahead of and behind the flying bat. In fact we have not yet succeeded in obtaining satisfactory directional measurements of the emitted intensity pattern from any bat, so that three dimensional triangulation faces unpredictable difficulties. New approaches, or much more diligent exploitation of old methods, are clearly needed.

The question of discrimination between the echoes from various targets is related to bats' resistance to jamming and to interference from extraneous noise in their own frequency range. In a jamming experiment such as those described by Griffin, McCue, and Grinnell (1963) echoes are discriminated from rather similar sounds, which may be pulsed or continuous. At first thought one might suppose that echoes of pulsed orientation sounds would be more difficult for a bat to distinguish from pulsed noise or clicks than from continuous noise. But jamming experiments with pulsed and continuous noise showed only small differences, and if anything the pulsed noise had a smaller jamming effect even though the off periods lasted only one to three milliseconds. The bats could also dodge wires much better after a restriction of the frequency band of the noise that left unmasked part of the two octave band through which their orientation sounds were sweeping.

We compared the results of experiments in our most effective jamming noise with predictions based on signal detection theory, and at the outset we assumed to simplify calculations that the air between echoing wire and listening bat was a single communication channel. But the bats detected wires about one tenth wavelength in diameter more successfully than is possible even for the "ideal detector" of signal detection theory! When the noise was sufficiently intense that it completely masked their whole frequency band, the bats turned to one final behavioral device which I failed at first to appreciate. In these jamming experiments the bats were forced to fly from end to end of a two by five meter flight chamber irradiated by noise from two arrays of loudspeakers, one at each end. When the noise was not too troublesome (even though on our oscilloscope the emitted pulses barely rose above the noise) the bats flew almost straight towards the ends of the flight space, dodging most of the wires as they would in the quiet. But when the noise became truly difficult they began to fly in zig-zag patterns and approached the wires so that wire echoes and jamming noise came from different directions. Its second ear allows the bat to compare the complexes of echo plus noise arriving over two channels and on this basis to detect faint echo signals otherwise hopelessly lost in the noise. One can draw an analogy here to the use of interferometry in detecting faint signals, except that these bats use brief pulses that produce non-overlapping echoes. Thus phase comparison in the usual sense is not available to them. But their neural processing must achieve comparable precision in selecting any available kinds of information that signal the presence of important small targets.

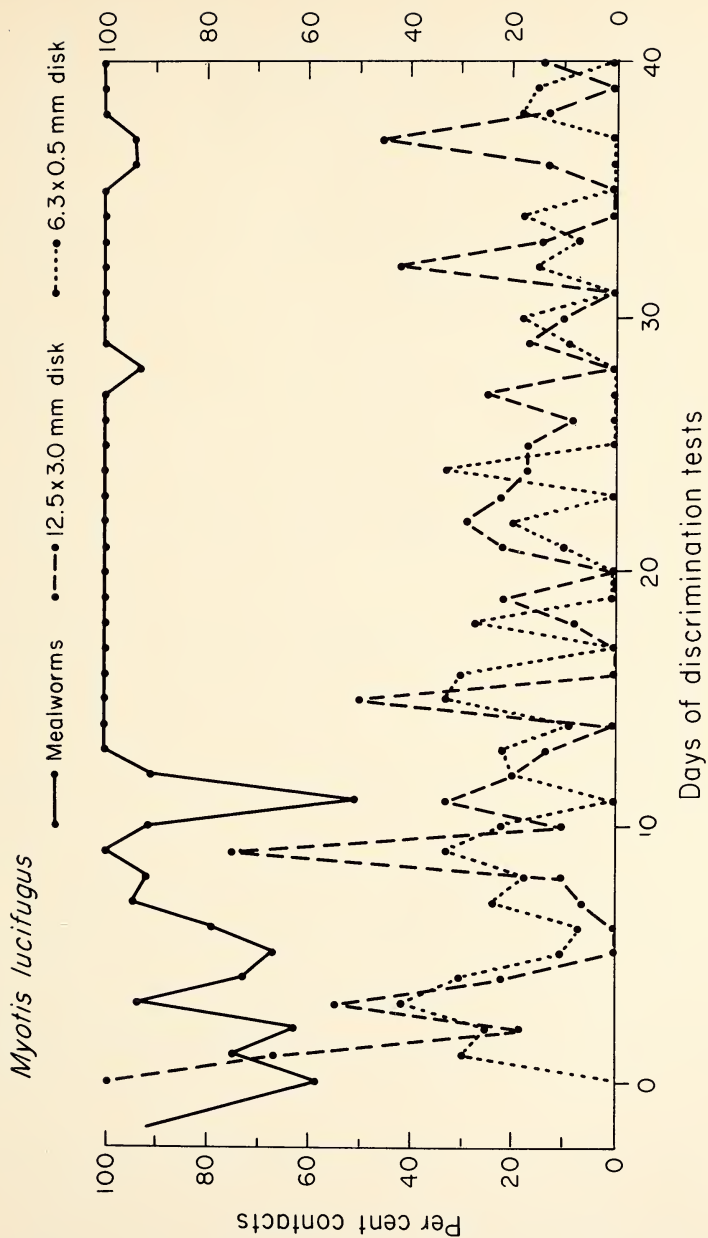


Fig. 1. Learning curve for an individual *Myotis lucifugus* that had been catching virtually every mealworm prior to day 0 when disks were first presented.

Having satisfied ourselves that the ability of bats to resist jamming could be reconciled with signal detection theory, I and several colleagues have turned in recent years to another type of orientation behavior in which bats appear to be incredibly proficient. While we lack any useful data on the selective capture or rejection of different kinds of insects under natural conditions, Suthers (1965) has shown that the fish catching bat Noctilio leporinus can learn to find food that is hidden just below the surface of the water by echolocating small markers protruding a few millimeters into the air. Contrary to some lines of speculation that appeared plausible before Suther's experiments (Griffin, 1958, pp. 224-228) these bats did not locate motionless and wholly submerged fish except by chance. But some of the markers they did learn to recognize were as small as 5 mm lengths of wire 0.21 mm in diameter. Suthers went on to train blinded N. leporinus to discriminate between two such 5 mm marker wires spaced 20 mm apart from a single slightly larger wire. A control experiment with two identical wires sloping in opposite directions yielded completely negative results, helping assure that cues other than echoes were not being supplied to the bats inadvertently. The echo intensities from single and double wires were very similar, but interference patterns produced distinctive directional echo patterns. Further work would be required to determine whether such geometrical fluctuations in echo pattern are actually exploited by these or other bats.

If one tosses a small pebble into the air near a bat that is foraging for insects, the pebble will often be approached and apparently attacked. Many sorts of small objects may elicit pursuit behavior,

sometimes with full catching maneuvers. The occasional hooking of a bat by a fly fisherman is more easily understood in view of Webster's electronic flash photographs that show how actively the tail and wing membranes are used in reaching out for insect prey and conveying it to the animal's mouth (McCue, 1961; Webster and Griffin, 1962; and Webster, 1963). When wild bats chase pebbles or when a captive bat accustomed to catching mealworms tossed up into a flight room eagerly pursues a tennis ball larger than its own body (Webster, 1963) it is natural to conclude that they have no powers of discrimination. When first observing the marked changes in tempo of bats' orientation sounds during normal insect hunting under natural conditions I never seriously considered the possibility of target discrimination. Yet we must recall our total ignorance about the insects that are caught, and still less about those that are ignored or rejected. Except under the special conditions where captive bats have been induced to catch selected insects, it is seldom possible to observe the insects at all. We can only infer that an insect was present when we see a bat execute a catching maneuver or hear the acceleration of the pulse repetition rate of its orientation sounds. To be sure Poulton (1929) analyzed the relative abundance of various species of moths in the piles of discarded wings under night roosts of Plecotus auritus, but some or all of the selection might have resulted from the bat's dropping or otherwise discarding certain moths after capture, rather than carrying them back to a roosting place to be devoured.

Webster's success in training Vespertilioidid bats such as Myotis lucifugus to catch mealworms tossed into the air allowed us to carry

out extensive studies of target discrimination under these somewhat artificial conditions (Griffin, Friend, and Webster, 1965). However far tossed mealworms may depart from any natural food or echolocation targets, it seems likely that the same adaptable hunting tactics and neural mechanisms were called into play as those that these bats have perfected for catching their food under natural conditions. We started with bats that had become so adept at catching mealworms that they almost never missed when hungry and when the larva was projected into space accessible to them. When inedible targets were first substituted for the expected mealworm almost anything was caught, or at least catching maneuvers were nearly the same up to the stage of actual contact with the wing or tail membranes. We could easily have become discouraged and concluded from the first few days' attempts that the bats could merely detect the presence and location of a small object but could not tell whether it was a mealworm, a piece of chalk, a marble, rubber band, or small coin. Only because Webster noticed that the hungriest bats did better than chance did we persist until, after several days, certain bats succeeded to varying degrees. The first extensive series of controlled experiments were those of Webster and Durlach (1963), in which a series of spheres were interspersed one at a time in a series of mealworms. The largest and smallest spheres were either rejected initially or after short learning periods, but spheres three to eight mm in diameter required many days of experience before the bats consistently rejected 80 to 100% of the spheres while catching an equally large proportion of the mealworms.

Various other targets were studied in a limited extent, and they were offered to the bats either simultaneously with one or more mealworms, or sequentially interspersed on irregular schedules one at a time so that the bat could not predict whether an edible or inedible target was next on our agenda. The results that seemed of greatest interest are already published in some detail (Griffin, Friend, and Webster, 1965) and hence the following discussion will avoid duplicating that paper, of which reprints are being furnished to those directly concerned with the discussion of the present paper. Two basic points merit elaboration, however, before discussing the apparently incredible nature of the bats' performance. First, these bats had learned to solve this particular discrimination problem during many days or even weeks of dealing with a hopelessly artificial situation. But it seems to me at least probable that the neural mechanisms in bats that are capable of learning to discriminate mealworms from disks can also learn to distinguish between edible and inedible targets under natural conditions. The second point is that the experienced bats made their choices at least as far from the targets as 40 or 50 cm, and did so before their orientation sounds had changed from what I and others have called the search phase. Specifically, the decision to catch or reject was made on the basis of echoes from the cruising type pulses that sweep from about 100 to 40 kc/sec. in a pulse duration of about two milliseconds. The much shorter, lower frequency, and much more rapidly repeated pulses of the terminal phase of "buzz" must serve some other

function than identification of the target as appropriate for capture or rejection -- at least under the conditions of these experiments.

We were able to obtain partly but not wholly satisfactory physical measurements of the echoes from mealworms and the disks used in these experiments as a function of angular orientation of the target with respect to the direction of sound incidence. Similar measurements have been reported by Dreher at a conference in New York in April 1965 (Dreher, 1966). He used sounds of longer wavelengths and targets of larger size and different shapes (cubes, spheres, cylinders, and pyramids). Instead of FM pulses he used a band of random noise almost seven octaves wide, then analyzed the echoes of this noise into 32 bands of equal width. A comparison of the relative echo intensities in these various bands showed some variation, and "echo signatures" which were not easily distinguishable even when each aspect as well as each target was considered as a separate species of echo. In studying Dreher's data I can see no way in which cubes could be reliably distinguished from spheres or pyramids without prior knowledge of the orientation of the target (base or edge toward the microphone, or intermediate positions).

The bats in our experiments lacked any basis on which to determine the target orientation of mealworm or disk. They simply heard a series of echoes which they were able to classify into two categories: "to be caught" and "not to be caught" and this classification was about 90% accurate. When we measured target echoes by setting up an "imitation bat" basically similar to Dreher's apparatus except that we used as

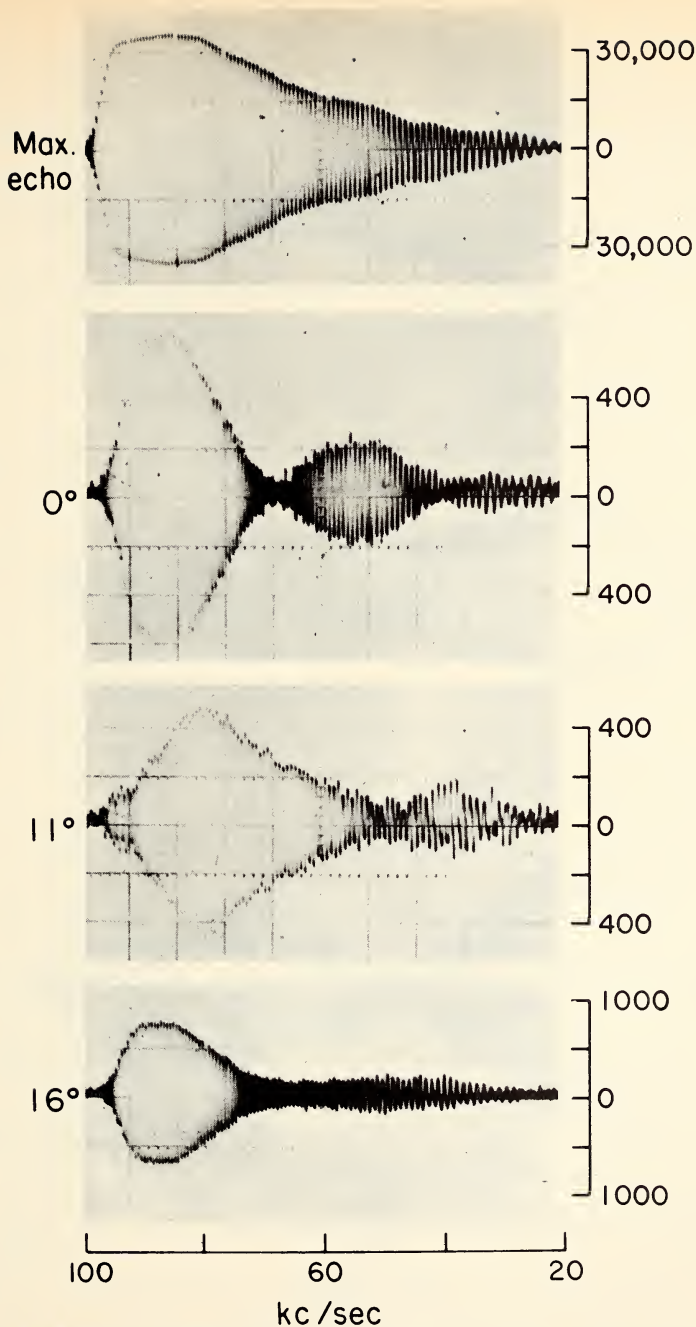


Fig. 2. Echoes of artificially generated frequency modulated pulses of sound closely resembling the orientation sounds of *Myotis lucifugus*. Amplitude scales are in arbitrary units, but these are consistent throughout Figs. 2 to 8. The "Maximum echo" was obtained from a sheet of stiff cardboard larger than the projected beam of sound adjusted to give maximum echo amplitude. Relative echo amplitudes discussed in the text and plotted in Figs. 5 to 8 were measured directly from cathode ray oscillograph records such as Fig. 2. For mealworms the designation of 0° was arbitrary.

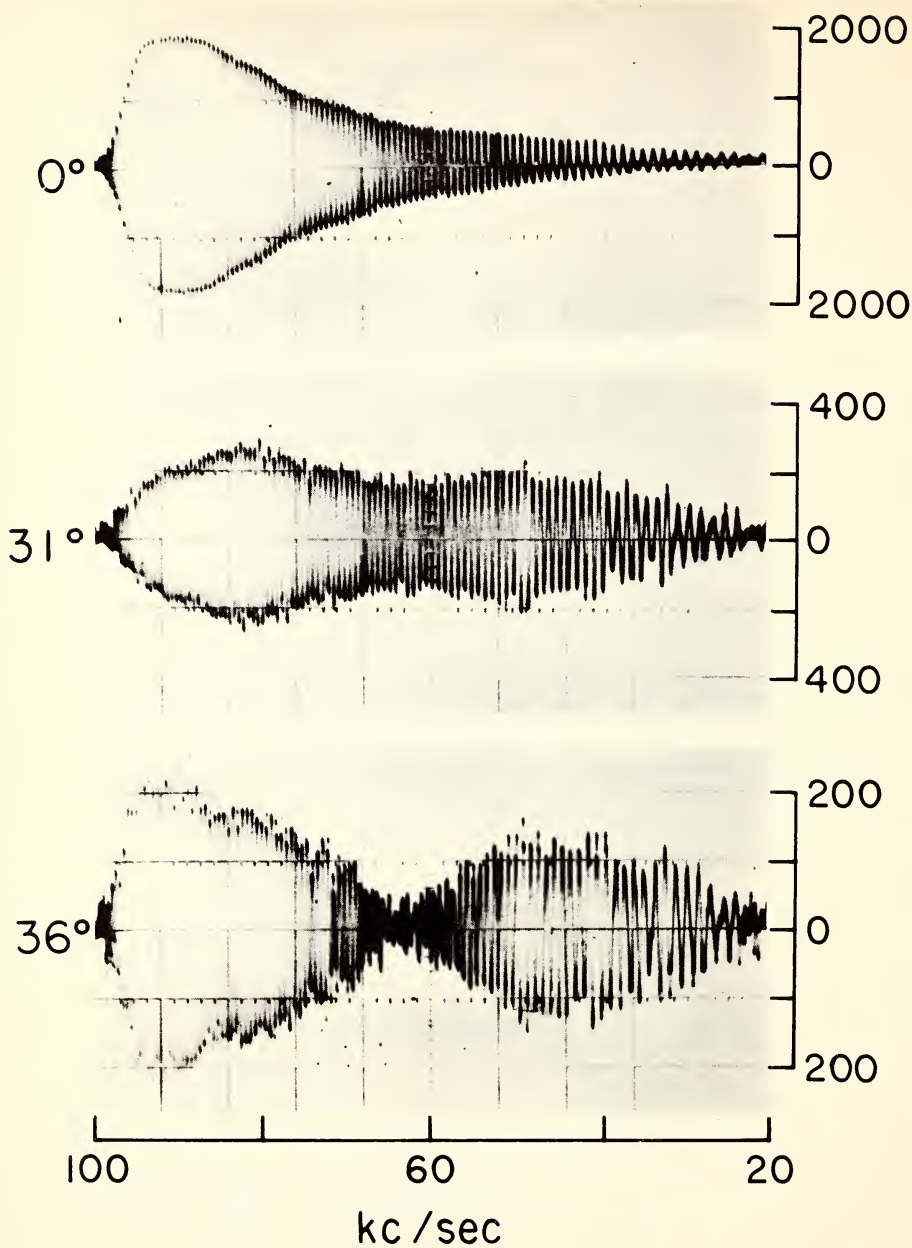


Fig. 3. Echoes like those shown in Fig. 2 but from a 0.5 X 6.3 mm disk.

nearly as practicable the same wavelengths, frequency sweep, and pulse duration as those actually employed by our bats to discriminate between the same targets. Working in an anechoic room, Dreher used 330 msec. pulses which overlapped extensively in time with the echoes from his test targets, although presumably the sound absorbant walls greatly reduced the direct signal from loudspeaker to microphone. We used pulses one or two milliseconds long at sufficient distances that there was no overlap between emitted pulse and returning echo. We found in preliminary measurements that constant frequency pulses yielded echoes that fluctuated enormously with minute changes in frequency or target orientation, due to interference patterns. FM pulses showed smoother variations without gross nulls, and presumably noise pulses would behave similarly. This may be an important reason why so many bats use FM or other types of broad band sonar signals. We presented data on the variation of echo level with target orientation from one typical case, (Fig. 3) and ranges of echo intensity variation for ten bands each eight kc wide (Fig. 2). Graphs similar to Fig. 3 for the other frequency bands showed equal or greater overlap in echo intensity between mealworms and disks.

Freedman (1962a, 1962b, 1963) has devoted considerable attention to the theory of echo formation, but he deals primarily with cases where the dimensions and radii of curvature of the targets are considerably greater than one wavelength. Bats work with wavelengths that approximate the dimensions of important targets. The theory of echo formation in this twilight zone between geometrical optics and scattering of waves

by objects much smaller than one wavelength seems to be complex and obscure. While somewhat repugnant to the orderly thinking preferred by physical scientists, we may be forced to analyze the anatomy of complex echoes if we wish to understand the successes of bats, cetaceans, or other animals that have become highly adapted for a life dependent on active sonar.

The "fine structure" of echoes

As a first step towards ascertaining which properties of echoes are used by bats to distinguish between similar targets I have recently analyzed in greater detail the measurements of mealworm and disk echoes discussed above. Adequate cues for the discrimination actually demonstrated by the bats do in fact appear to be present in the patterns of echo spectra.

It is important to realize that these discriminations are difficult achievements that a bat must learn. A typical learning curve is shown in Fig. 1.

In these measurements the targets had been suspended by very fine wires from a large C shaped frame so that frequency modulated pulses of sound very similar to those used by our bats impinged on the target and returned echoes to a microphone about 15° to one side of the loudspeaker. This angular separation was the smallest practicable with available equipment, but it considerably exceeded the comparable angle between a bat's mouth and ears. This degree of approximation to natural conditions appears adequate in the present state of our knowledge (or better, our ignorance); but in future improvements on these experiments the physical acoustics of the bat's head should be copied more faithfully. Echoes from the frame and the bare wires

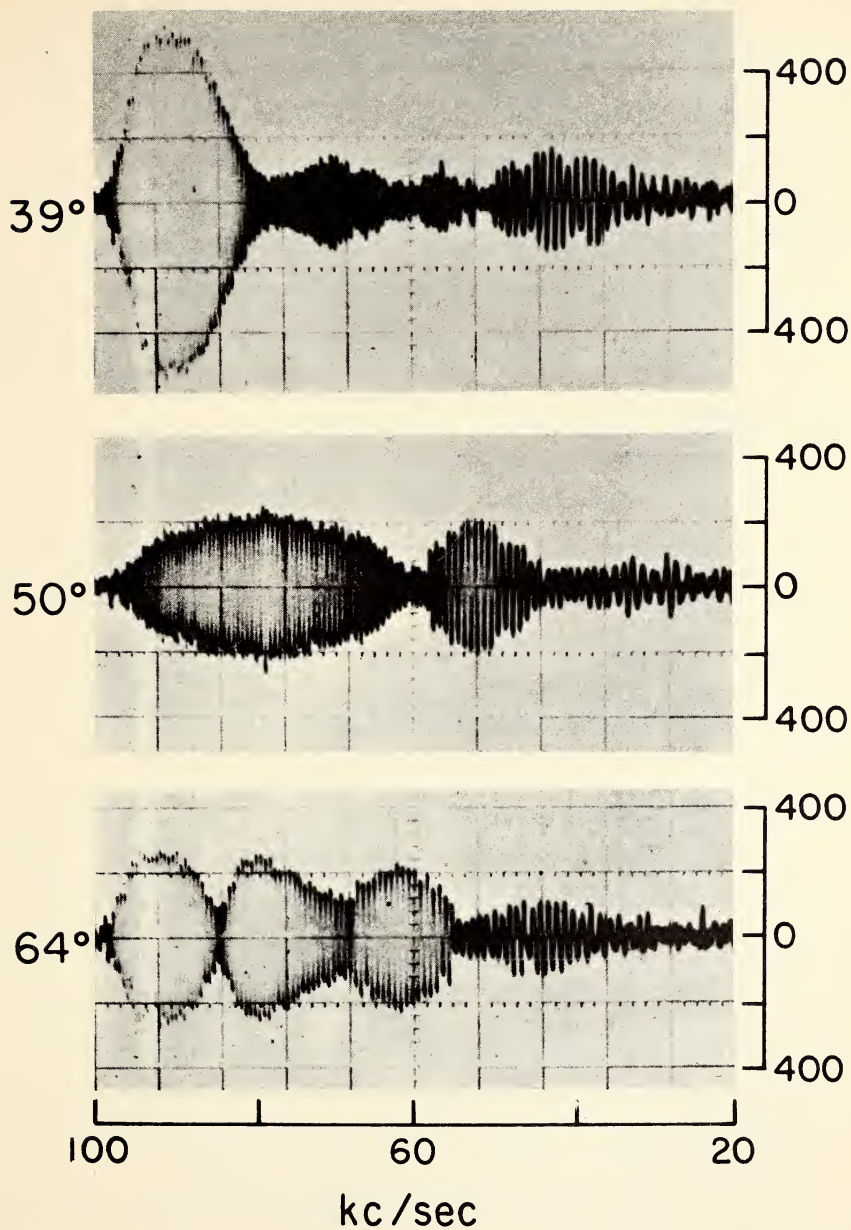


Fig. 4. Echoes like those shown in Fig. 2 but from 3.0 X 12.5 mm disk.

were below noise level. The frame was so mounted that the target could be rotated without moving it enough to alter appreciably the echo of a spherical test target of comparable size.

The echoes were photographed from a cathode ray oscilloscope and compared with what I have called the "maximum" echo obtained with the same apparatus when the target was replaced by a large surface of hard cardboard oriented roughly perpendicular to the sound beam and adjusted to give the maximum possible echo intensity. Such a maximum echo is shown in the top trace of Fig. 2; frequency is plotted horizontally, decreasing from left to right as a function of time. Each pulse had a duration of 1.9 msec, thus approximating the duration and rate of frequency sweep of the actual orientation sounds of the bats that made the actual discriminations. Immediately below the maximum echo are echoes from a mealworm in three angular orientations that demonstrate a characteristic variation of echo anatomy. Zero degrees was an approximate optimum angle giving a strong echo at most frequencies. From 0° to 11° the two peaks shifted to distinctly lower frequencies and dropped somewhat in amplitude, but in the next five degrees of rotation the high frequency peak grew in amplitude and shifted back to higher frequencies. For a 0.5×6.3 mm disk the echo variation was more rapid with respect to intensity but somewhat smoother with frequency, as exemplified by the records for 0° and 31° in Fig. 3. The change between these two angles was relatively gradual, but between 31° and 36° a null developed at about 60 kc (the noise level was about 30 of the arbitrary units of these graphs). A third typical example of the variation of echo with frequency and target orientation is shown in Fig. 4.

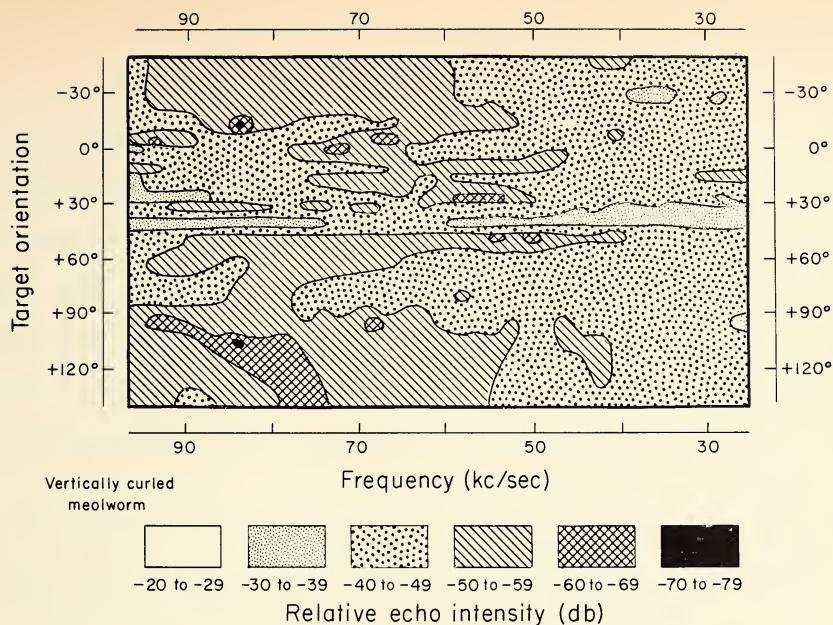


Fig. 5. Contour plot of relative echo amplitudes for a mealworm curled vertically, as a function of frequency and target orientation.

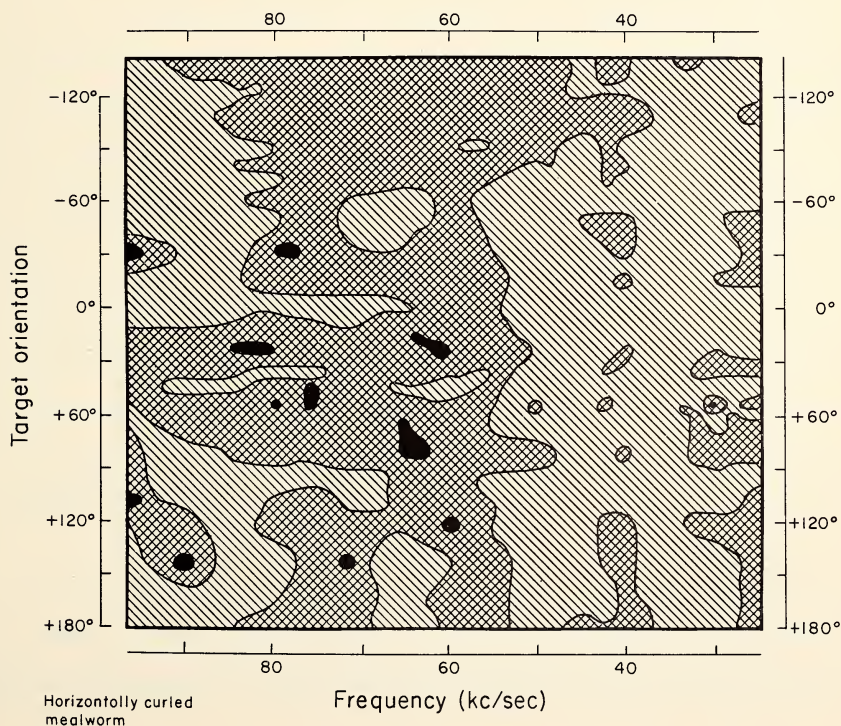


Fig. 6. Contour plot of relative echo amplitudes for a mealworm curled horizontally. The amplitude intervals are the same as in Fig. 5.

It would obviously be helpful to visualize the full pattern available to the bat's auditory system, and hence the oscilloscope was photographed at all apparent maxima and minima and whenever a change in echo spectrum appeared to have developed as the target was gradually rotated. From these photographs the echo level was measured in decibels relative to the maximum echo, at intervals of 2 kHz from 96 to 26 kHz. The resulting numerical data were then tabulated with frequency horizontal and angular orientation of the target vertical. The resulting tables were of course unwieldy, having approximately 30 rows and columns. One convenient method of visualizing such a mass of data is a contour map in which a given range of echo intensities is represented in the same manner that conventional contour maps represent land between certain limits of elevation above sea level.

Such an "echo contour map" for a mealworm is presented in Fig. 5, with each shaded area representing a ten decibel range of echo intensity, relative to the maximum echo described above. Frequency is plotted horizontally just as in the oscillograms of Figs. 2 to 4. The vertical ordinate is the angular orientation of the mealworm over a range of roughly 180°. The shading of the various areas represent the echo intensity, the strongest echoes being shown by white, next most intense by light gray and so on through darker grays, and finally black for the minimum measurable echoes. Within each ten decibel area there were of course many minor hills and valleys, and in future analyses of this type a careful choice of contour interval might bring out a more accurate rendition of echo anatomy.

It may well be asked whether such a contour map has any relevance to the actual processes in a bat's brain by which echoes are analyzed. We know

from the neurophysiological experiments of Grinnell and Suga that action potentials from the brains of anaesthetized bats show differential responses to frequency and intensity that are more than sufficient to analyze echoes with the degree of resolution displayed in this contour map. Indeed tonotypic organization of the mammalian auditory system at several levels is well established, so that we can even imagine a neural surface in which evoked potential amplitude would vary in some such way.

But having accepted echo contour maps such as Fig. 5 as graphic representations of stimulus properties that could be analyzed by a bat's brain, we must face two serious limitations of available data of this kind. The first is the fact that only a part of the vertically plotted range of target orientations would be available to a bat in the fraction of a second between hearing the first echo and committing itself to attack or ignore a given target. Any one FM echo would be represented by a line or very narrow horizontal band across one of these contour maps. The targets certainly turned and tumbled as they rose and fell, as shown in several multiple flash photographs taken during the experiments, but the rate and extent of angular change were not at all adequately measured in a sufficient number of specific cases when other relevant events were simultaneously recorded with the necessary accuracy. My best guess is that in most cases roughly 60° of target rotation would have been covered by successive echoes before the bat began its reaction of attack or avoidance.

A second dilemma is presented by the irregular geometry and echoing cross section of mealworms. When straight they approximate cylinders and those used in these experiments were 2 to 3 mm in diameter and 16 to 23 mm

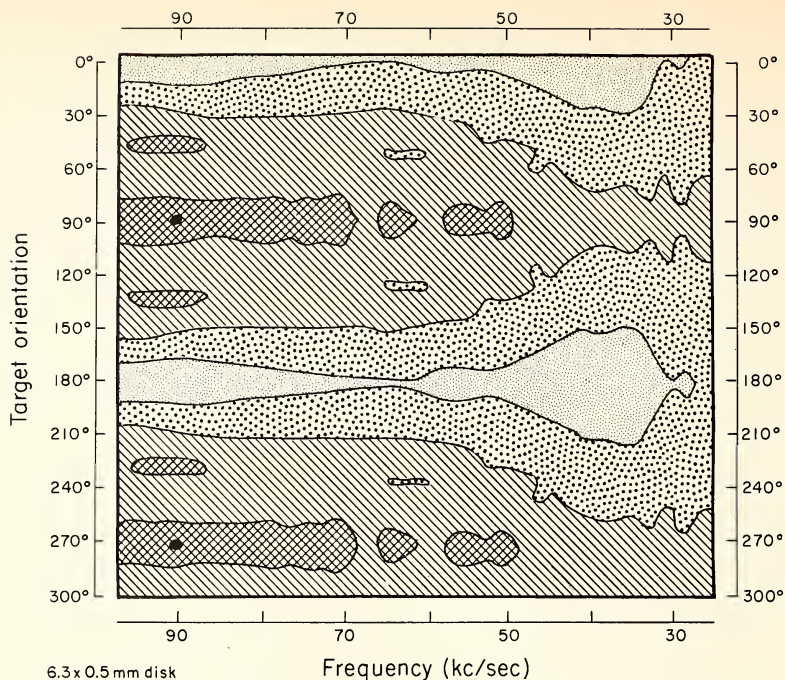


Fig. 7. Contour plot of relative echo amplitudes for a 0.5 X 6.3 mm disk. The amplitude intervals are the same as in Fig. 5.

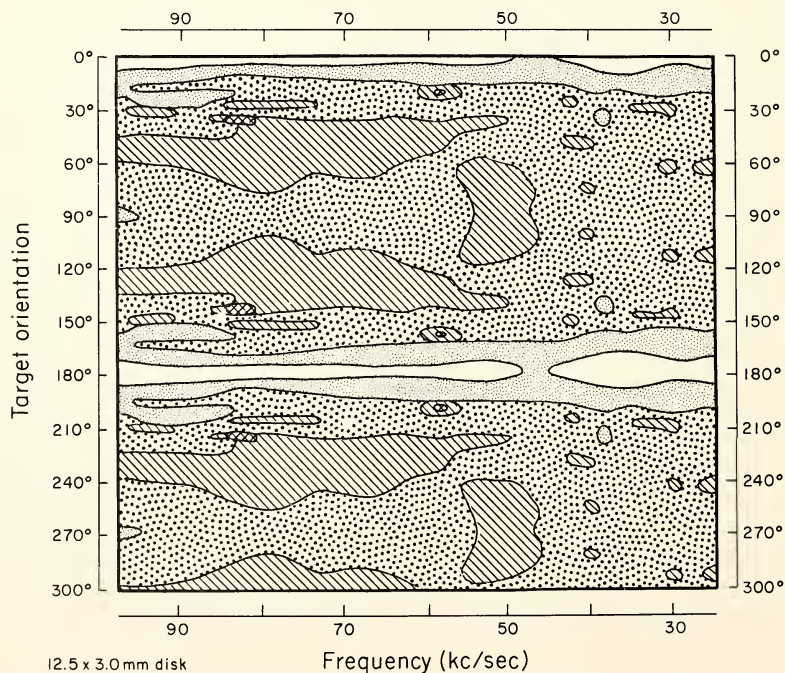


Fig. 8. Contour plot of relative echo amplitudes for a 3.0 X 12.5 mm disk. The amplitude in tervals are the same as in Fig. 5.

in length. But they very often curled their bodies to varying degrees, and the echo varied considerably with the degree of curl and the orientation of the plane of curling. For our most extensive echo measurements a typical degree of curling was selected, and a typical mealworm was held either with the plane of curling horizontal or vertical. Since our artificial bat-like sounds were projected horizontally, the horizontally curled mealworms presented a more nearly constant cross-section and their echoes were usually weaker. Fig. 6 shows a contour map similar to Fig. 5, but for horizontally curled mealworms rotated about an axis lying in the plane of curl and passing roughly through the center of the body. Again the approaching bat might have available for analysis an arbitrary sample of roughly 60° out of such a contour map as Fig. 5 or 6. But it is most important to remember that these are merely arbitrary samples from a large population of echo contour maps -- a sample far from sufficient to characterize reliably mealworm echoes even under the restricted conditions of our experiments. Yet real echoes of flying insects encountered under natural conditions must vary even more widely, as measured by Roeder (1963). The moving wings of natural targets may well give them highly characteristic though equally heterogeneous echo contour patterns.

Disk echoes are shown in the same way in Figs. 7 and 8. They too are complex patterns, but unlike mealworm echoes, or those from flying insects, they have a regular pattern of repetition every 90° of rotation, and all axes of rotation give the same echo pattern, whereas flying insects must yield echoes that vary extensively not only with wing movements but almost as much with body orientation relative to the direction from which the bat's orientation sounds arrive.

In studying these echo contour maps it is tempting to imagine that one can discern a "diskishness" common to Figs. 6 and 7, as contrasted to "mealwormishness" in Figs. 4 and 5. But in view of the limitations discussed above, such qualitative judgments are highly questionable. There is, however, one simple criterion that might be applied both by zoologists and by the bats. This is the rate of variation of echo level with target orientation or with frequency. Perhaps disk echoes are smoothly and monotonously rolling surfaces like the tops of stratocumulus clouds viewed from an airplane window while mealworm echoes may resemble the ragged and chaotic landscape of the moon. If this were the bat's criterion, a simple average of echo variation with target orientation, or with frequency, might show a sufficiently consistent difference to allow mealworms to be discriminated from disks as accurately as the bats actually did demonstrate that they could do. The large table on which Figs. 4 to 7 were based was used to compute the average of the changes in echo level between adjacent rows and columns. The results of this averaging are listed in Table 1. Judging by our limited sample of mealworm echo contours, it is interesting to note that the average angular variation of echo level would be grossly unreliable, but that the average variation with frequency does appear to provide an adequate criterion (disks 0.70 and 0.90 versus horizontally and vertically curled mealworms 0.97 and 0.99 dB per kHz respectively). Thus a bat might be imagined to judge as edible those targets whose echoes varied with frequency by more than 0.95 dB per kHz, while rejecting targets with smaller average variation values. Of course it is frequency that is systematically scanned by each pulse.

While this explanation seems as good as any, my principal conclusion is that these measurements should be considered provocative rather than satisfying. Their chief value is to help clarify what sorts of improved experiments and measurements are called for in the future.

Table 1. Average variation in echo intensity of mealworms and disks as a function of frequency and of target orientation. The frequency intervals were in all cases 2 kHz. Target angle intervals were variable, but most were about 10 degrees. Since maxima and minima were especially selected for photography of the cathode ray oscilloscope, there is some bias in the data favoring sharp shifts in echo amplitude with target orientation. Such a bias would tend to increase the average values slightly compared with an analysis based on equal angular intervals.

<u>Target</u>	<u>Average change in echo level per degree change in target orientation (dB)</u>	<u>Average change in echo level per kHz change in frequency (dB)</u>
Thick disk (12.5 X 3.0 mm)	0.83	0.90
Thin disk (6.3 X 0.5 mm)	0.44	0.70
Vertically curled mealworm	0.71	0.99
Horizontally curled mealworm	0.30	0.97

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Abstract

Myotis lucifugus trained to catch mealworms tossed into the air can be further trained to discriminate by echolocation between a roughly cylindrical mealworm and a disk of similar dimensions. The previous analysis of the echoes from these targets reported by Griffin, Friend, and Webster (J. Exptl. Zoology, 158, 155 - 168, 1965) showed extensive overlapping in echo intensity between the echoes of disks and mealworms at all frequencies employed by these bats (25 to 100 kHz). These measurements have been extended to include three dimensional plots of echo intensity as a function of frequency and target orientation relative to the direction of incident sound. While the available data are limited to two arbitrary degrees of curling of the mealworm, they suggest that the pattern of echo variation with changing target orientation may provide the type of acoustic fine structure by which the bat can identify such targets.

DISCUSSION

by

R. S. MACKAY

One cannot criticize an excellent summary such as this, but a few points were brought to mind for discussion. The frequency modulated or "chirp" pattern of frequencies in the echo-ranging sounds has been mentioned. Especially when the outgoing and returning pulses overlap, it is tempting to ascribe the reason for this frequency modulation to ranging schemes in which frequency scanning to a "resonant" condition exists, or else a frequency differing process could indicate range. But such a process could also serve quite a different purpose. One normally thinks of a sharp pulse being used to indicate range in an echo location process in order to define time intervals sharply. If this sharp pulse is run through a dispersive filter, then out will come an extended pulse containing a succession of frequencies, or a chirp. This chirp can be emitted from a transducer that radiates sound. This sound signal can later be collected, transduced, and run back through a corresponding filter to reconstitute a sharp pulse well defined in time. (The pulse duration can be longer than the transit time). The point of this procedure is that the sound producing mechanism is able to radiate a considerable amount of energy with a much lower peak power. Thus in a demanding situation, such a procedure might yield an improved signal "without straining the vocal cords", i.e. one can obtain more energy in a power-limited system. Note also that the range of intensities to which the sound sensing mechanism is exposed is also reduced by spreading a given energy signal over a longer period, and thus the possibility of linear functioning is increased. Physiological mechanisms to perform such an analysis can certainly be imagined, and such an explanation for these procedures should not be ignored.

As Dr. Griffin has noted, the wavelengths employed approximate the dimensions of the insects being pursued (whether one considers the velocity of sound in air or in tissue, this is approximately true). Thus the bat may sweep frequency to produce resonances in its target; if nothing else, this could strengthen the return signal and give further information about target size. Such a procedure might be considered as equivalent in the case of vision to looking at an object with a

particular color of light, scanned to bring out a particular property.

The necessity for continuously recording the position of a subject has been emphasized. A number of possibilities suggest themselves, and the one of choice probably depends upon the amount of such analysis that is to be done. For limited experiments, the laborious task of analyzing motion pictures frame-by-frame is probably justified rather than making a big expenditure on special equipment. If much work is to be done, then some alternative is justified. Though many species of bat are quite small, a high frequency tunnel diode oscillator could be carried by most; phase comparison at several radio receivers would then allow exact localization. One could instead place several oscillators around the room, with reflections in the radio pattern giving a measure of position. Most of the familiar schemes of radio navigation could be considered here, at appropriately higher frequencies. One would probably prefer not to use sound waves in such observations in order to avoid interference with the animals. A small light affixed above the animal's back could probably be viewed during most maneuvers by three photomultipliers at the ceiling. A simple comparison circuit would then indicate exact position because of the inverse square law giving a ranging action. To use transit time effects with light would require very precise circuits which would be quite expensive. Perhaps the best system, after all, is to take motion pictures of the activity, and then analyze these as automatically as is justified. Object tracking circuits can be built, but the human eye is really a very good tracking device. Thus a person's eyes could undoubtedly accurately follow an object in a moving picture, especially one already once seen. Thus the electrical potentials of oculography might be recorded to indicate object position while a subject (with head fixed) was watching a motion picture of the flight experiments. A second person could be simultaneously watching the insect, with his separate potentials recorded appropriately.

With regard to the fishing bat, I wonder if Dr. Griffin has any indication if the bat perhaps senses the wake of moving fish; such a wake can be remarkably persistent once generated.

It was noted that bats work with wavelengths that approximate the dimensions of important targets. It is perhaps not true that the theory of echo formation in this range is obscure, though in any particular case, the details may be more complicated. One thing can be said, and that is that the magnitude of the returned signal varies greatly with small changes in object dimension, and without the monotonic change as a function of size. However, even this could be useful in some cases. Thus a motion of the target would yield a large change in the signal returned to the bat, and during a long pulse, target shape might be indicated by the temporal pattern of intensity changes with changing orientation. Similarly, the wing beat of flying insects might give a more pronounced signal to a bat using a frequency whose wavelength was of the same order as the dimensions of the insect's wings. It would be interesting to throw up test targets for inspection both tumbling and in a pure translational trajectory.

I am pleased that the role of two ears has been mentioned. There are a number of cases in which one could conceive of the rejection of reverberation from a true signal by having noise phase out between a pair of ears. It should be noted that there is even some acoustic direction finding ability by a human subject in water, though this ability is considerably reduced from functioning in air, and thus it is obvious that aquatic animals could use similar processes, especially with appropriate isolation of two or more hearing organs.

DISCUSSION

by

W. K. GRIMLEY and E. J. RISNESS

To a worker in the sonar field, the parallels with bat echolocation are remarkably close. In both instances there is an initial phase of search and classification, for which broadband signals are used to extract the utmost information about the target. Once the target has been assessed as a true one, the "tracking" phase is entered. Here the object is to retain bearing information, and for this purpose a very short pulse and high repetition rate are used, to increase both the data rate and the signal-to-background ratio. Again, in both fields, it seems that target manoeuvre is used as an additional and important classification clue. It would seem that this latter adequately explains the observations on the ability of the bat to discriminate between mealworms and other objects. The untrained bat relies essentially on the "flight-path" of the target - anything that rises and then falls will be attacked. With experience, he learns to use subtler clues, such as "echo quality". There is a very close analogy here with the behaviour of human sonar operators.

Finally, in both fields we are working in the region so aptly described by the author as the "twilight zone" where neither geometrical optics nor large-wavelength approximations fully apply, and sonar research workers, as much as the bat investigators, are vitally concerned with the anatomy of complex

echoes.

Some details in the paper arouse interest. The statement that bats are better than "ideal detectors" is surprising, to say the least. However, it is understood that, when directional effects are taken into account, the observed detection rate is reconcilable with signal detection theory.

Much play is made in the paper of the fact that echoes are generally non-overlapping, and that hence such features as phase correlation and Doppler cannot be used. The argument appears to be that for an instrument to compare non-overlapping pulses it would be necessary to introduce time delay (e.g. to produce a correlogram, or to "mix" the signal with a reverbant echo to estimate Doppler). It is not clear, however, that such physical delays are necessary, since the brain has a memory (which may indeed represent a real delay loop). For example, a human being has no difficulty in assessing the frequency shift between two widely separated pulses - indeed, with training, a memory of pitch can be extended over hours or days. Similarly, it is not impossible that a comparison of pulse shapes might be accomplished by a feat of memory.

On the instrumentation side, it is somewhat surprising that it appears to have been so difficult to use a multiple receiver location technique, even with the wide variations in signal level that are quoted. The difficulty appears to lie in the difficulty of establishing corresponding points on the echoes received at spaced hydrophones, so that time-differences cannot be measured accurately. One would not have expected this to be an insuperable difficulty, and in the worst case, there are well established

correlation techniques for "lining up" pulses.

The recent experimental work on the ability of the bat to discriminate similar targets (discs or mealworms) is of great interest. Although it was not possible to record the echoes actually heard by the bat while making this discrimination, similar echoes were recorded separately. It would be of some interest to see whether automatic pattern recognition techniques, of which there are many examples today, could succeed in distinguishing between the two types of target to anything like the extent achieved by the bat. The comparatively limited amount of information in an acoustic echo (as compared with visual patterns, for example) may ease the problem of finding an encoding of the data suitable for such pattern recognition techniques.

RÉSULTATS MÉTROLOGIQUES EXPÉRIMENTAUX DE L'ÉCHOLOCATION CHEZ LE *PHOCAENA PHOCAENA*, ET LEUR COMPARAISON AVEC CEUX DE CERTAINES CHAUVES-SOURIS

par
R.G. BUSNEL et A. DZIEDZIC

INTRODUCTION.-

L'étude comparative de l'écholocalisation dans le règne animal est encore à faire, faute d'une expérimentation systématique et analogique sur les différentes espèces actuellement connues qui utilisent ce procédé de détection. Dans ce travail, nous avons voulu jeter les premières bases d'une telle analyse, en nous référant d'une part à nos propres travaux sur un Dauphin, et à ceux de GRIFFIN et de son école sur certaines Chauves-Souris. Les protocoles d'expériences conçus indépendamment par les deux groupes de recherches ont suffisamment de points communs entre eux, pour que certains des résultats soient rapprochés et discutés comparativement. Ce genre d'approche du problème paraîtra peut-être un peu audacieux à certains ; nous l'avons tenté et nous pensons qu'il est valable pour découvrir des points communs à des systèmes qui utilisent des signaux très différents et dans des milieux différents, et ce afin de permettre peut-être l'atteinte des lois physiques et mathématiques communes aux divers systèmes d'écholocalisation animaux. Nous sentons combien il pourrait être prématuré d'en tirer des conclusions définitives mais cet essai nous a paru nécessaire.

Dans une première partie, on comparera le seuil de détection des obstacles, et dans la seconde, on comparera l'étude des variations de la fréquence de répétition des impulsions en fonction de la distance animal-cible.

Dans une autre note, l'un d'entre nous développera un certain nombre de considérations mathématiques, physiques et psychophysiologiques, se rapportant à divers aspects de ces deux problèmes.

Travaux principalement entrepris à la Station Océanographique Anton Bruun, STRIB, Danemark - dépendant du Laboratoire d'Acoustique Animale de l'Ecole Pratique des Hautes-Etudes, avec l'aide de l'I.N.R.A., du C.N.R.S., de la D.R.M.E. (Contrat n° 64-34092-00-480-75-01), de l'O.T.A.N., de l'O.N.R. (Contrat n° 62555-3637) et de l'Université de Copenhague.

A. - Seuil de détection d'obstacles filiformes par
Phocaena phocaena.

Comme ceux des autres Delphinidae, les signaux d'écholocation utilisés par le Phocaena phocaena sont des impulsions brèves à spectres de bruit, d'une durée de 1,2 ms, en moyenne, comprise entre 1 et 3 ms.

Par ailleurs, si chez de nombreuses espèces comme le Tursiops truncatus, le Delphinus delphis, les Globicéphales ou le Steno bredanensis par exemple, ce spectre de fréquence est très large, il s'étend en effet au delà de 200 kHz. chez le Steno (14) et le maximum d'énergie des impulsions se trouve centralisé entre 10 et 30 kHz. Les études analytiques des signaux de Phocaena montrent que les composantes fréquentielles d'intensité maximale sont comparativement très basses puisqu'elles se situent vers 2 kHz. seulement, et la bande totale de fréquence ne semble pas dépasser quelques dizaine de kHz.

Ces divergences de structure se rencontrent d'ailleurs chez d'autres espèces animales, aériennes ou terrestres et à titre indicatif on a regroupé dans le tableau 1 et pour certaines d'entre elles, les caractéristiques principales des signaux d'écholocation qu'elles utilisent.

Actuellement, il apparaît que dans le processus qui entre en jeu dans l'écholocation utilisée par les différentes espèces de Mammifères marins, la largeur et la densité du spectre, aient un rôle capital dans la discrimination à courte distance des cibles et obstacles de faibles dimensions et qu'elles délimitent le seuil de leur perception.

Mais, si de nombreuses expériences sur le pouvoir de localisation et d'évitement des obstacles ont été réalisées sur les Chauves-Souris, en particulier par GRIFFIN et ses collaborateurs d'une part (6-7-8), MÔHRES d'autre part (11-12), qui ont rapporté des résultats précis sur le seuil de détection de certaines espèces de ces animaux, aucune expérience analogue n'a encore, à notre connaissance, été réalisée sur des Delphinidae. Seule KELLOGG (9-10) et NORRIS (13) ont abordé ce problème sur le Tursiops, d'un point de vue plus global et sans encore avoir rapporté des

résultat quantitatifs sur les limites de discrimination de ce Dauphin.

Pour notre part, nous avons réalisé ce travail sur Phocaena phocaena, qui avec son système à relativement faible largeur de bande, apparaissait, à priori, comme devant être peu perfectionné.

Les résultats de cette étude sont rapportés dans la présente note, ils montrent qu'à courte distance le pouvoir de perception et de localisation par écholocation seule du Phocaena est très remarquable, lui permettant d'éviter des fils dont le diamètre est très inférieur à la longueur d'onde des signaux ayant été enregistrés avec notre appareillage dont la limite supérieure était de 50 kHz. (Tolana - Type ERM 850).

Protocole expérimental*

Les tests ont été faits avec une femelle adulte de 35 kg. et 1,40 m. de long, dans un bassin rectangulaire de 54 m² et 1,20 m. de profondeur.

Des fils de 1,50 m. de long étaient suspendus à 5 glissières disposées parallèlement à l'un des côtés du bassin, à 1,80 m. au-dessus de la surface; la distance entre chaque glissière était d'environ 1,50 m., tandis que les fils de chaque rangée ainsi constituée étaient distants de 1 m. les uns des autres. Le nombre total d'obstacles était de 30.

Un jeu de cordage permettait de déplacer horizontalement chacune des rangées, de 10 cm. de part et d'autre d'une position centrale, et d'immerger verticalement les fils jusqu'à ce que leur extrémité inférieure affleure le fond du bassin.

* Les auteurs remercient vivement MM. S. ANDERSEN, E. LESCOMBE et D. RIVIERE qui ont grandement contribué à la réalisation de ces expériences.

Avant l'expérimentation, on aveuglait l'animal par des coupelles en caoutchouc de 6,5 cm. de diamètre (technique de NORRIS), et on immergeait les fils ainsi que 4 gros obstacles, 2 flottants, 2 fixes; ces derniers étaient destinés à modifier la configuration générale du bassin, et désorienter l'animal. L'ensemble des fils immergés formait une figure en quinconce, et l'animal laissé libre de nager dans le bassin, devait louvoyer pour les éviter.

Deux épreuves journalières de 30 mn. chacune étaient imposées à l'animal; une le matin, l'autre l'après-midi; pour chacune d'elle le diamètre et la nature des fils étaient constants, mais la géométrie de la position des obstacles était toujours différente.

Chaque épreuve complète comportait deux phases, la première d'environ 20 mn. pendant laquelle l'animal était aveuglé; la seconde d'une durée moindre, 10 mn. environ, pendant laquelle, l'animal ayant eu ses coupelles enlevées, se déplaçait en utilisant à la fois ses systèmes d'information auditif et visuel.

Pendant chaque séance on enregistrait d'une part sur un magnétophone Nagra III B, les émissions sonores de l'animal, d'autre part, les indications de l'observateur qui relevait les évitements ou les accrochages des obstacles par l'animal; pour chaque période de travail le nombre moyen de passages entre obstacles était d'environ 300. Ces bandes ont ensuite été dépouillées à l'enregistreur de niveau Brüel et Kjaer, ce qui a permis de déterminer le pourcentage des évitements par rapport aux accrochages, c'est-à-dire l'acuité de détection pour des obstacles de nature et de diamètres donnés, séparément pour l'animal aveuglé et normal.

On a ainsi testé, en fonction de leur diamètre, des fils de fer, de cuivre et d'acier de forte densité, respectivement 7,8 - 8,9 - 7,7; puis des fils de nylon monobrisés et de perlon torsadés tribrisés, dont la densité est voisine de celle de l'eau (1,09).

Par ailleurs, on a déterminé la probabilité de rencontre des obstacles non détectés, en plaçant les repères à quelques centimètres au-dessus de la surface du bassin, et en notant chaque passage et accrochage qui se serait produit si les

files avaient été immergés et non détectés par l'animal.

RESULTATS

1) Comportement de l'animal :

Du point de vue comportemental, il convient de noter que dans toutes les phases expérimentales où l'animal n'était pas aveuglé, sa vitesse de nage était plus grande que dans celles où il était contraint d'utiliser son système d'écholocation seul. On a pu estimer ainsi que sur l'ensemble des tests, l'animal nageait environ 2 fois plus vite dans les premiers cas que dans les seconds.

De même, dans le cas d'utilisation du système d'écholocation seul, la vitesse de nage était plus grande lorsque la détection était bonne, tandis que lorsqu'elle était défectueuse, l'expérimentateur devait encourager fréquemment l'animal à se déplacer.

2) Niveaux acoustiques :

Aucune tentative de masquage acoustique n'a été faite, et, dans l'ensemble des tests, le niveau général du bruit de fond du bassin a été réduit au minimum, par la suppression de l'écoulement de l'eau et les bruits extérieurs. La valeur moyenne du niveau de ce bruit, déterminée à partir des enregistrements, a été de l'ordre de 35 dB réf. 2.10^{-4} barye. L'intensité des signaux émis par l'animal était généralement constante, de l'ordre de 70 dB réf. 2.10^{-4} barye. Toutefois, un accroissement d'environ 30 dB a été remarqué fréquemment lorsque l'animal accrochait un obstacle.

Des variations dans la cadence d'émission des impulsions ont été également observées lors de l'approche des obstacles par l'animal.

3) Détection des obstacles :

Les résultats obtenus montrent que dans le cas des files métalliques, le pourcentage des évitements par rapport aux accrochages n'est pas modifié par la nature spécifique du métal utilisé ; c'est-à-dire que pour ces matériaux dont la densité relative est élevée (supérieur à 7) une augmentation de cette dernière de 1 g/cm^3 n'apporte pas un accroissement de la puissance des échos, qui soit perceptible par l'animal.

Tableau 1

	Oiseaux	Mammifères terrestres					Mammifères marins	
		Volants			Non Volants		Tursiops	Phocaena
		Vespertilionidae (3-6-15-16-17)	Rhinolophidae (17-18)	Rousettus (11-12)	Sorex (5)	Tenrec (4)	(9-19)	(1-2)
Fréquence composante kHz.	4 à 5 6 à 10	30 à 120	85 à 100	6,5 à 120	30 à 60	5 à 17	20 à 100	1,5 à 4
Durée de l'impulsion en ms.	32 (moyenne) 5 (moyenne)	1 à 4	10 à 100	5,5 (moyenne)	0,75 à 33	0,1 à 0,3 (minimum)	1	1,2 à 3
Fréquence de répétition en kHz.	5,5 à 10 4 à 590	3 à 200	5 à 80	5 à 80	7	?	10 à 400	20 à 560 (moyenne) à 736 (maximum)

Tableau 2 : ANIMAL AVEUGLE

Diamètre des obstacles	4	3,5	3	2,8	2	1,9	1,8	1,6	1,5	1,4	1,25	1,2	1,0
-1-	1351	694		964	362				1147			720	1298
-2-			276				442						120
-3-						457		454		585	390		284
Evitements - E -													
-1-	14	8		17	31				12			60	71
-2-			19				67						77
-3-						14		15		14	8		10
Accrochages - A -													
-1-	0,11	1,15		1,76	8,56				1,05			8,33	5,48
-2-			14,5				15,1						64
-3-						3		3,3		2,4	2,4		3,5
A - E -													
-1-	99,89	98,85		98,24	91,44				98,85			91,67	94,52
-2-			85,5				84,9						36
-3-						97		96,7		97,6	97,6		96,5
Evitements en %													
-1- Fils métalliques													
-2- Fils nylon monobrin													
-3- Fils perlon 3 brins													

Tableau 2 : ANIMAL AVEUGLE (Suite)

Diamètre des obstacles	0,9	0,8	0,75	0,6	0,5	0,35	0,20
-1-							
-2-		580	792	837	713	785	77
-3-							
Evitements - E -	61						
	432	29					
Accrochages - A -		43	42	97	65	165	38
-1-							
-2-	30						
-3-	10	12					
A E		7,41	5,3	13,8	9,1	21,02	54
-1-							
-2-	49						
-3-	2,3	41,5					
Evitements en %		92,59	94,70	81,2	90,4		46
-1-							
-2-	51						
-3-	97,7	58,5					

-1- Fils métalliques

-2- Fils nylon monobrin

-3- Fils perlon 3 brins

Tableau 3 : ANIMAL NON AVEUGLE

Diamètres: obstacles	4	3,5	3	2,8	2	1,9	1,8	1,6	1,5	1,4	1,25	1,2
-1-	774	706		864	323				792			683
Evitements - E -			256				305					
-3-						417		588		554	534	
Accrochages - A -	4	6		6	15				6			23
-2-			0				6					
-3-						2		2		3	3	
$\frac{A}{E} \%$	0,52	0,85		0,69	4,65				0,76		3,36	2,42
-1-							1,98					
-2-						0,48		0,34		0,54	0,56	
-3-												
Evitements en %	99,48	99,15		99,31	96,35			99,24				96,64
-2-			100				98,02					
-3-						99,52		99,66		99,46	99,44	
-1- Fils métalliques				-2- Fils nylon monobrin				-3- Fils perlon 3 brins				

Tableau 3 : ANIMAL NON AVEUGLE (Suite)

Diamètre des obstacles	1,0	0,9	0,8	0,75	0,6	0,5	0,35	0,20
-1-	1035		203	802	833	566	694	92
Evitements	-2-	155	23					
- E -	-3-	780	610	602				
Accrochages - A -	-1-	25		7	19	81	34	148
	-2-	52	15					
	-3-	5	4	25				
$\frac{A}{E}$ %	-1-		3,45	2,36	9,70	6,01	21,3	22,4
	-2-	33,5	65					
	-3-	0,64	0,65	4,15				
Evitements en %	-1-	97,58		99,65	97,60	90,30	93,99	78,70
	-2-	66,5	35					
	-3-	99,36	99,35	95,85				
1- Fils métalliques	-2- Fils nylon monobrin				-3- Fils perlon 3 brins			

-1- Fils métalliques

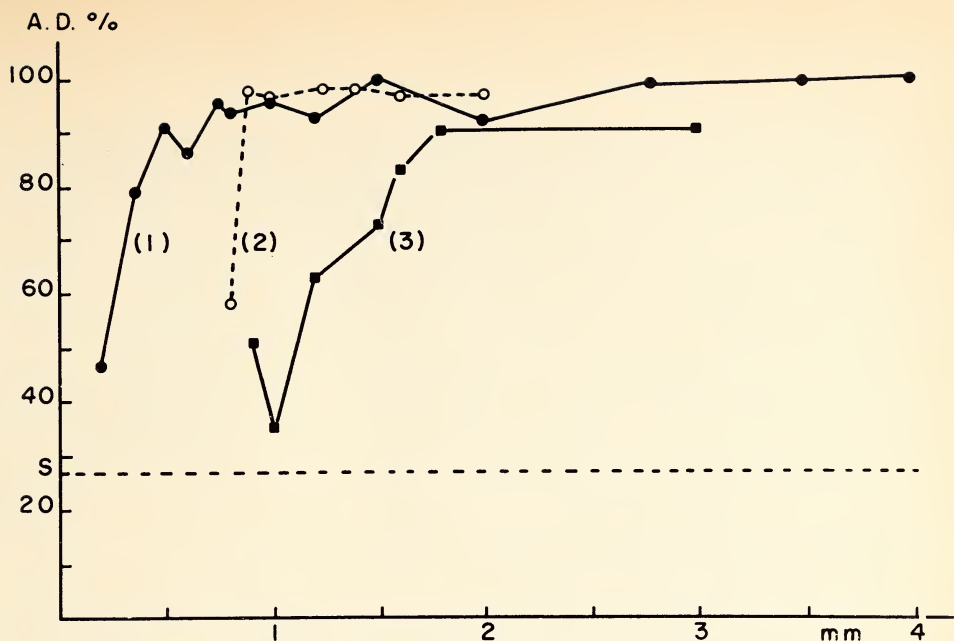


Fig. 1.- Acuité de détection par écholocation seule d'obstacles filiformes de différents diamètres par *Phocaena*.

- 1 - fils métalliques.
- 2 - fils perlon torsadés trois brins.
- 3 - fils nylon monobrin.

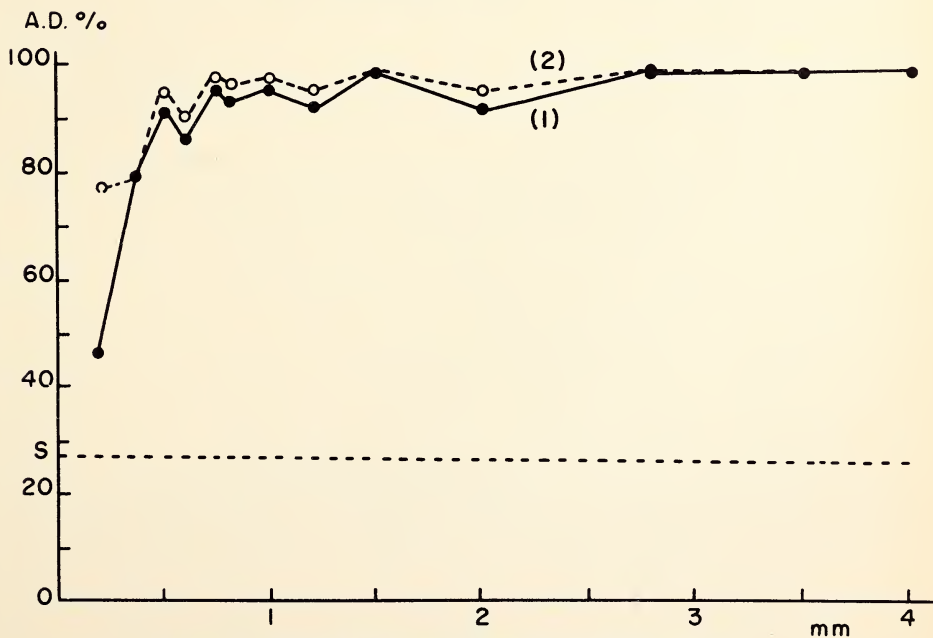


Fig. 2.- Acuité de détection des fils métalliques de différents diamètres par *Phocaena*.

- 1 - écholocation seule utilisée.
- 2 - écholocation et vision utilisées simultanément.

Par contre près du seuil, la géométrie de l'obstacle semble avoir une influence importante sur l'acuité de détection; en effet, dans le cas du nylon monobrin et du perlon torsadés sont nettement mieux détectés que les autres comme le montrent les courbes expérimentales 2 et 3 de la Fig. 1, où le tracé 1 représente les résultats obtenus avec les fils métalliques. Sur cette figure, on a porté en ordonnées, les pourcentages des évitements par rapport aux accrochages, c'est-à-dire l'acuité de détection A.D.; et en abscisses les diamètres des fils en millimètres. Si l'on considère que la valeur de A.D. = 50 % représente le seuil de détection, les diamètres correspondants sont alors:

- pour les fils métalliques : environ 0,2 mm
- pour les fils perlon torsadés : environ 0,8 mm
- pour les fils de nylon monobrin : environ 1 mm.

Les résultats obtenus avec un animal non aveuglé, c'est-à-dire, utilisant son système audio-visuel complet, ne sont que faiblement améliorés par rapport aux précédents comme le montrent les deux courbes de la Fig. 2, relatives à ces deux situations de l'animal et pour des fils métalliques. Les données exactes correspondant à chacune des diverses conditions expérimentales sont rapportées dans les tableaux 2 et 3.

4) Valeur expérimentale de la probabilité de la rencontre des obstacles :

Avec les repères non immergés, les valeurs expérimentales obtenues lorsque l'animal utilise à la fois son système visuel et son système auditif, sont les suivants :

Nombre de passage	:	1 353
Evitements	:	784
Accrochages	:	569

ce qui donne un pourcentage d'évitements de 27 %.

Ces résultats montrent que :

1° L'acuité de la détection décroît rapidement près du seuil. Une diminution du diamètre des fils métalliques de 0,3 mm. (de 0,50 à 0,2 mm.) fait tomber le pourcentage des

 N° 1
 N° 2

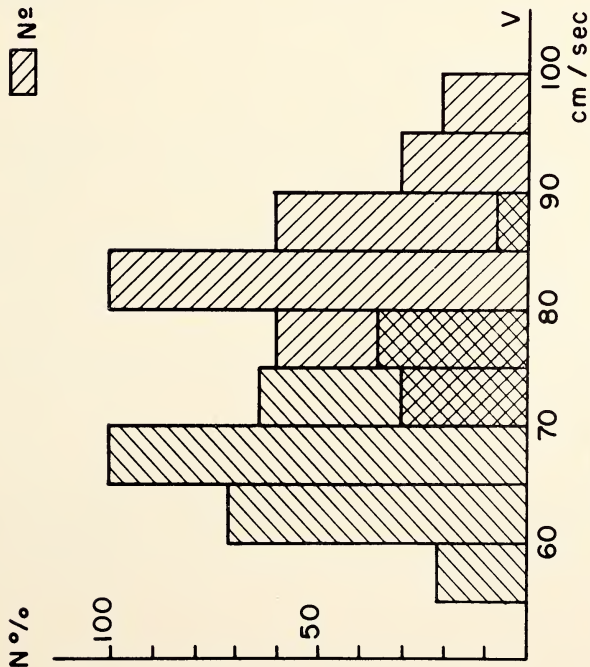
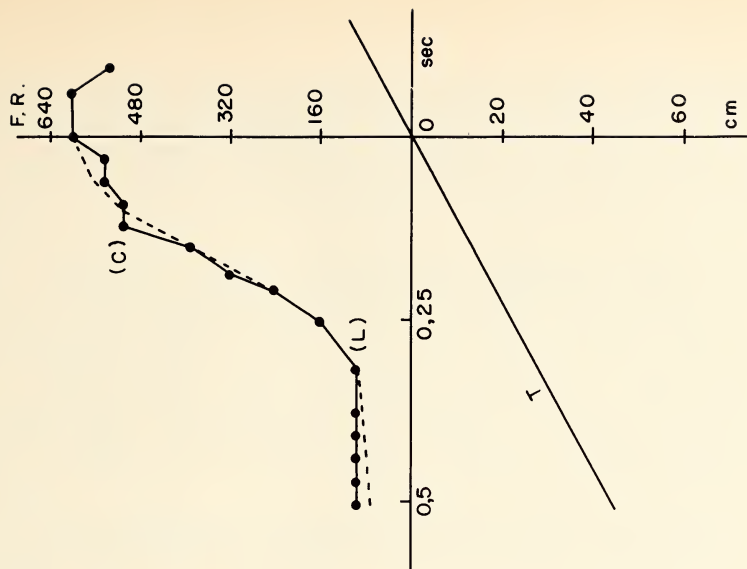


Fig. 3.- Histogramme des vitesses de nage de deux Phocaena lors de l'approche d'une cible alimentaire.

n° 1 - animal 1.
 n° 2 - animal 2.



D.-A.B.

Fig. 4.- Distribution type de la fréquence de répétition des impulsions d'écholocation lors de l'approche d'une cible alimentaire par Phocaena.

évitements de 90 à 50 %, soit une chute de 40 %; tandis que dans le cas des fils de perlon torsadés, cette chute est encore plus accentuée, puisqu'on trouve la même valeur de 40 %, pour une diminution du diamètre de 0,1 mm. seulement.

2° Le cas du nylon monobrin semble être un peu différent car si la chute près du seuil semble relativement plus faible, le pourcentage d'erreurs reste élevé, même pour des fils de diamètre important; il est en effet de 30 % pour les fils de 3 mm. de diamètre. Ceci peut être attribué en particulier à la grande transparence acoustique du matériau, qui n'est pas compensée par la forme géométrique, comme dans le cas du perlon torsadé 3 brins.

3° Si l'on considère les caractéristiques acoustiques des matériaux utilisés, résumées dans le tableau ci-dessous, on voit qu'une différence d'impédance caractéristique de 12.10^6 unités S.I. entre le fer et l'acier n'apporte pas de modification notable dans l'acuité de détection au voisinage du seuil.

Matériau	Eau de mer à 20°	Nylon	Acier	Fer	Cuivre
Masse spécifique g/cm ³	1,02	1,09	7,7	7,8	8,9
Vitesse de propagation longitudinale m/s	1,513	2,620	5,100	3,400	3,500
Impédance caractéristique (unités S.I.)	$1,54.10^6$	$2,86.10^6$	$39,2.10^6$	$27,3.10^6$	$31,2.10^6$

Comparaison des performances obtenues avec celles connues de certaines Chauves-Souris.

L'expérimentation décrite n'a pu être faite que sur un seul animal et les résultats obtenus ne peuvent être qu'indicatifs. Toutefois, comme aucun travail analogue n'a été, à notre connaissance, réalisé sur d'autres espèces d'animaux marins qui utilisent l'écholocation, ces résultats peuvent servir de point de comparaison pour de futures investigations. Il conviendrait alors, que la surface équivalente des cibles utilisées puisse être parfaitement connue, ce qui n'est pas le cas ici, et l'emploi d'obstacles de forme géométrique simple bien définie, comme par exemple des sphères, doit être préconisé. On peut, pour l'instant, confronter les résultats acquis avec le Phocaena à ceux de certaines Chauves-Souris, particulièrement Myotis lucifugus et Plecotus auritus obtenus par GRIFFIN et ses élèves dans des expériences analogues.

D'après ces auteurs, les seuils de détection se trouvent pour ces 2 espèces compris entre 0,07 et 0,12 mm. pour la première et 0,28 à 0,35 mm. pour la seconde; pour chacune d'elles, les fréquences composantes moyennes des impulsions d'écholocations étant 55 et 30 kHz, ce qui correspond à des longueurs d'onde de 6,25 et 11,5 mm.

On voit ainsi que si l'on ne tient compte que de la composante maximale de ses signaux d'écholocation (2kHz), le Phocaena phocaena aurait a priori un système inférieur à celui des autres Delphinidae, mais qu'il serait néanmoins apte à détecter des obstacles filiformes métalliques dont le diamètre est 3750 fois inférieur à la longueur d'onde de cette composante (chez Myotis lucifugus le diamètre minimum détectable est environ 100 fois inférieur à la longueur d'onde du signal). Néanmoins, il a été montré que les impulsions d'écholocation du Tursiops, du Steno et d'autres Delphinidae, comportent des composantes spectrales élevées, 208 kHz chez le Steno par exemple, dont la directivité est très prononcée (14). On doit donc penser, (l'appareillage utilisé ne permettant pas d'études analytiques au-delà de 50 kHz) qu'il en est de même chez Phocaena et que dans ces conditions, ces composantes spectrales élevées contribuent, à courte distance, mais d'une manière importante, à l'accroissement de l'acuité de détection par écholocation.

B. - Variations de la fréquence de répétition des impulsions d'écholocation en fonction de la distance animal - cible.

Il est un fait d'observation que dans la majorité des cas, les espèces qui utilisent l'écholocation, augmentent la cadence de leurs émissions au fur et à mesure qu'ils se rapprochent d'un obstacle ou d'une proie. On a pu vérifier qu'il en était de même pour Delphinus delphis (20) et Phocaena phocaena (1,2). Ce phénomène peut théoriquement s'expliquer par une nécessité pour l'animal, d'augmenter la précision de la localisation, quand la distance qui l'en sépare d'une cible donnée diminue, et ce en augmentant le nombre d'informations par unité de temps. Cet accroissement serait alors directement lié à la précision de la détection.

Des observations préliminaires ont montré que les émissions d'écholocation sont toujours utilisées par le Phocaena aveuglé ou non lors de l'approche et de la capture d'une proie, donnée au cours du nourrissage, et on a tenté, sur cette espèce, de déterminer expérimentalement la variation de la cadence des émissions, en tenant compte d'une part de la vitesse de nage des animaux et d'autre part de leurs distances instantanées à la cible.

Protocole expérimental :

Un poisson qui constitue la cible, tenu à la main, est immergé à 15 cm. de profondeur environ. Il est présenté à l'animal qui doit, pour l'atteindre, parcourir toute la longueur du champ d'une caméra cinématographique fixée perpendiculairement à 2 m. au-dessus de la surface du bassin ; la vitesse de prise de vue était de 32 images par seconde. Une règle graduée de 5 cm. en 5 cm. parallèle au déplacement habituel de l'animal, et visible dans l'objectif de la caméra, a permis, à partir du film ainsi obtenu et examiné image par image, de connaître les distances instantanées de l'animal à la cible.

Par ailleurs, à partir des oscillogrammes des enregistrements sonores, pris en synchronisme avec la caméra de prise de vue, il était possible, par la confrontation de ces deux films, de calculer la vitesse d'approche de l'animal ainsi que le nombre d'impulsions émises par image, soit toutes les 1/32 sec.

Cette expérience a été faite dans un bassin de 54 m² et 1,20 m. de profondeur sur 2 femelles adultes l'une de 165 cm. de long pesant 71 kg, l'autre de 161 cm. et 68 kg. Au total, environ 200 approches ont été ainsi filmées et enregistrées.

Le matériel utilisé était, d'une part, une caméra Pathé Webo 16 mm. f = 25, d'autre part, un magnétophone Nagra III B, un hydrophone HP 40 et un amplificateur de 100 kHz de bande passante.

Résultats:

a) Vitesse d'approche vers la proie:

On a constaté que pour les deux animaux, au début du nourrissage, des variations relatives importantes (jusqu'à 30 %) des vitesses instantanées de nage avaient lieu; une rapide stabilisation se produisait ensuite, dès la 5ème prise au maximum, et, qu'alors, les approches se faisaient à vitesse pratiquement constante.

Les valeurs maximales des vitesses instantanées ont été pour chacun des deux animaux de 180 cm/s. environ.

Dans le cas où les approches étaient régulières ($dv < 10 \%$) soit au total 52 pour l'animal n° 1 et 34 pour l'animal n° 2, les vitesses se répartissent régulièrement autour de 67,5 cm/s. et 82,5 cm/s. respectivement ainsi que le montrent les 2 histogrammes de la Fig. 3.

b) Variations de la fréquence de répétition des impulsions:

Dans la majorité des cas, où la vitesse d'approche pouvait être considérée comme constante, la distribution de la cadence de répétition en fonction du temps (c'est-à-dire de la distance de la cible) obtenue à partir des oscillogrammes, obéit à une loi similaire à celle trouvée dans des expériences analogues sur certaines chauves-souris. La Fig. 4 donne un exemple type obtenu sur Phocaena. On voit ainsi que l'allure générale de cette distribution est celle d'une 1/2 courbe en cloche dont le maximum est atteint au moment de la prise de la proie. La partie inférieure, pratiquement horizontale où la fréquence de répétition est faible (20 imp./s. environ) s'incurve rapidement en un point (L) alors que l'animal se trouve à une distance de quelques

Tableau 4 : POINT DE LOCALISATION (L)

Animal n° 1	118	121	124	128	129	131	133	140	141	148
Test n°										
Distance de la proie (cm/sec)	32	32	26	30	34	31	26	29	24	20
T. précédant la capture (sec.)	0,44	0,47	0,38	0,4	0,5	0,38	0,38	0,4	0,3	0,35
F. instantané d'émission (imp/sec.)	128	192	192	64	96	128	96	64	64	96

Tableau 4 : POINT DE LOCALISATION (L) (Suite)

Animal n° 2	4	5	6	8	9	10	12	13	15	16	17	18
Test n°												
Distance de la proie (cm/sec.)	25	27	30	29	24	25	11	25	23	26	24	27
T. précédant la capture (sec.)	0,30	0,28	0,34	0,35	0,31	0,29	0,14	0,34	0,3	0,38	0,38	0,38
F. instantané d'émission (imp./sec.)	80	96	110	160	128	80	128	96	128	128	128	128
Test n°	20	30	32	35	36							
Distance de la proie (cm/sec)	27	35	37	23	26							
T. précédant la capture (sec.)	0,34	0,38	0,4	0,25	0,3							
F. instantané d'émission (imp./sec.)	128	128	160	128	96							

Tableau 5 : POINT DE DECISION (C)

Animal n° 1	121	124	128	129	131	133	140	141	148
Test n°									
Distance de la proie (cm/sec)	10	4,5	5	6	3	6	8	2	8
T. précédent la capture (sec)	0,16	0,07	0,09	0,09	0,035	0,09	0,11	0,026	0,14
F. instantané d'émission (imp./sec.)	640	580	512	580	544	512	430	575	416

Tableau 5 : POINT DE DECISION (C) (Suite)

Animal n° 2	4	5	6	8	9	10	12	13	15	16	17
Test n°	4	5	6	8	9	10	12	13	15	16	17
Distance de la proie (cms)	5	6	10	4	7,5	6	2	11	0	6	7
T. précédant la capture (sec)	0,06	0,066	0,13	0,047	0,09	0,066	0,025	0,16	0	0,085	0,09
F. instantanée d'émission (imp./sec.)	515	480	480	512	450	432	384	480	480	480	416
Test n°	18	20	30	32	35	36					
Distance de la proie (cms)	4	5	7	8	4	5					
T. précédant la capture (cm/sec)	0,056	0,077	0,06	0,09	0,043	0,06					
F. instantanée d'émission (Imp./sec.)	480	375	512	512	512	416					

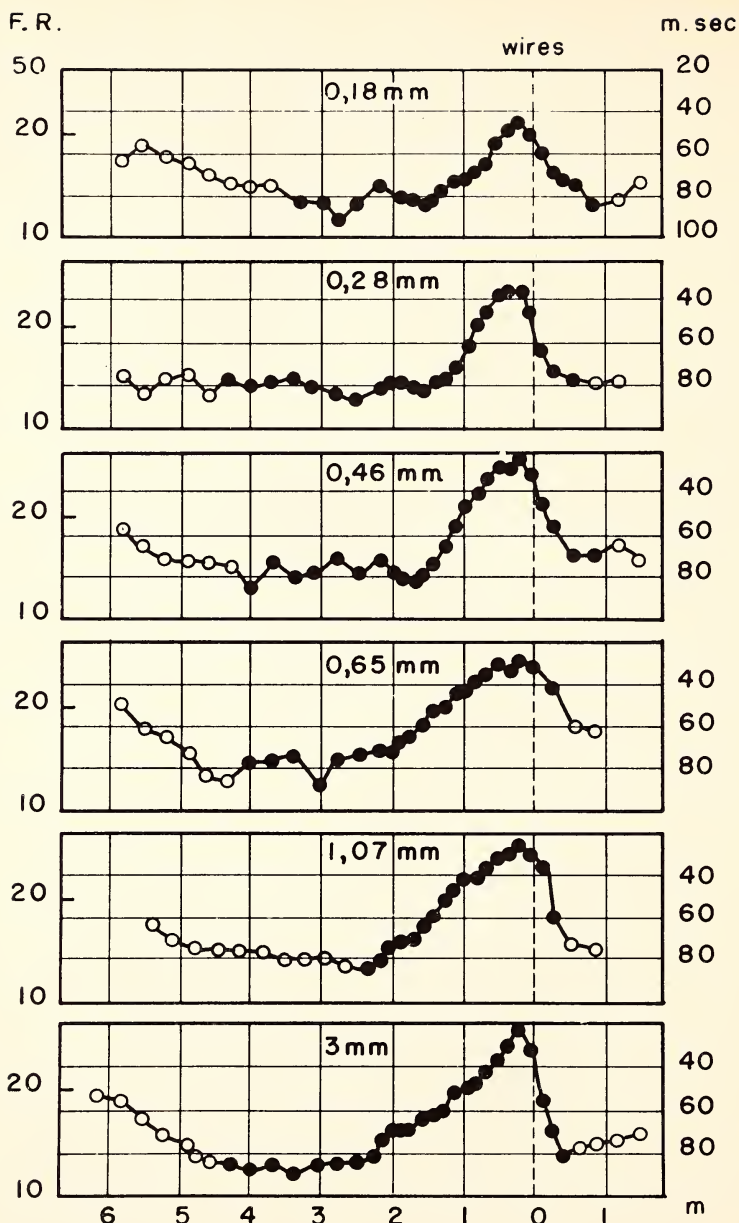


Fig. 5 : Expériences de Griffin et Grinnell sur la chauve-souris (voir texte).

dizaines de centimètres de la proie (20 à 40 cm.). L'inclinaison de la partie ascendante qui suit et qui est d'autant plus forte que le point (L) se trouve près du but diminue ensuite à partir d'un point (C) qui correspond à une distance animal - proie inférieure à 5 cm., mais reste positive jusqu'à l'instant de capture.

En aucun cas, il n'a été possible d'observer une interruption de l'émission lors de la prise de la proie, qui est toujours suivie d'un ralentissement rapide de l'émission et d'une stabilisation à la cadence minimum de quelques dizaines d'impulsions par seconde.

Pour la commodité de l'exposé, on appellera le point (L) point de localisation et le point (C) point de décision. Ils doivent en effet avoir leur importance dans l'approche; et l'on peut penser que le premier correspond à une localisation et une reconnaissance suffisante de la cible pour permettre à l'animal d'orienter son déplacement, tandis que le second peut être interprété de deux manières, c'est-à-dire soit comme une saturation mécanique de l'organe d'émission, soit comme un acte réflexe se produisant à l'instant où la proie convoitée est suffisamment proche et bien localisée pour que l'animal amorce le mouvement de capture.

Les coordonnées de ces deux points pour certains tests typiques et pour les deux animaux, sont données dans les tableaux 4 et 5.

A titre de comparaison, on donnera ici (courbes de la Fig. 5) les valeurs obtenues par GRIFFIN et GRINNELL (6-7-8) dans des expériences sur Chauves-Souris dont le protocole était très similaire au nôtre.

Fréquence de répétition maximale :

a) Cas des Chauves-Souris

D'après les observations sur l'évitement des obstacles par les Chauves-Souris, réalisées par GRIFFIN et GRINNELL (7-8), le point de localisation (L) variable avec les approches (comme dans nos expériences sur *Phocaena*), était généralement compris entre 230 et 53 cm., tandis que contrairement à nos observations la fréquence maximale (environ 200 impulsions par seconde pour *Eptesicus*) était émise alors que les

animaux se trouvaient encore à quelques centimètres des obstacles (15 à 20 cm.), distance à laquelle les animaux amorçaient leur mouvement de passage des obstacles.

Sur ces tracés (Fig. 5), le point de décision (C) est également apparent; on peut donc penser que chez la Chauve-Souris, ces deux points ont une signification semblable à celle donnée plus haut pour le *Phocaena*, c'est-à-dire que le point (2) doit correspondre, avec une assez grande vraisemblance, à l'instant de décision par l'animal de poursuivre son approche, tandis que le point (C) qui peut en particulier, correspondre à une limitation physiologique, du système émetteur ne peut pour l'instant que recevoir une interprétation hypothétique.

b) Cas du *Phocaena*

Chez le *Phocaena*, la fréquence maximale de répétition est généralement atteinte au moment de la capture de la cible par l'animal, et ce n'est généralement qu'après que la décroissance de la cadence de l'émission a lieu. Il y a donc une différence importante entre les deux cas expérimentaux et il semble qu'étant donné la différence comportementale des animaux dans chacune de ces expériences, c'est à elle que doit être imputée ce décalage temporel où la fréquence de répétition atteint son maximum.

Dans le tableau suivant sont rapportées les valeurs des fréquences de répétition maximales obtenues par les deux animaux, respectivement sur 16 et 23 approches différentes, les valeurs moyennes correspondantes sont 560 et 562 impulsions par seconde, soit un intervalle de temps minimum entre impulsions légèrement inférieure à 1,8 ms. Comme la durée des impulsions au moment de la prise de la proie est de 1,2 ms. environ, c'est donc un intervalle de 0,6 ms. qui sépare 2 impulsions successives. On peut alors penser que la fréquence de répétition maximale observée, doit représenter une valeur au delà de laquelle l'émission devenant pratiquement continue, perdrait les propriétés informationnelles propres aux impulsions. En dehors de ce fait, la limitation de la fréquence de répétition pourrait également être due non pas au système émetteur, mais au système récepteur. En effet, elle pourrait en particulier être due à un phénomène de fusion auditif, du genre flicker, dont l'approche du seuil entraînait la limitation; à titre indicatif, chez l'homme, l'intervalle de temps minimum perçu entre deux impulsions à front raide est voisin 1,14 ms. (Lafon, communication personnelle)

Dans le tableau n° 1 où sont données différentes caractéristiques des impulsions d'écholocation, utilisées par des Oiseaux, des Mammifères terrestres volants et non volants, ainsi que des Mammifères marins, on remarque que :

- a) la valeur maximale de la fréquence de répétition est obtenue chez le Phocaena, chez lequel la composante spectrale d'intensité maximale est plus basse (1,5 à 4 kHz).
- b) dans l'ensemble c'est chez les Delphinidae que cette fréquence maximale de répétition est la plus élevée.
- c) mais que Steatornis, dont la fréquence spectrale d'intensité maximale est relativement basse (6 à 10 kHz), émet également à forte cadence de répétition.

CONCLUSION. -

Les résultats expérimentaux rapportés ici sont relatifs au Delphinidae Phocaena phocaena.

Ils comportent deux types d'expériences qui mettent en évidence :

- 1) la finesse de l'acuité du système d'écholocation d'un animal aveuglé, mesuré par sa capacité d'évitement d'obstacles filiformes, de nature et de diamètre connus ;
- 2) la comparaison entre la valeur de perception uniquement par système d'écholocation, et celle obtenue avec le même animal ayant son système audio-visuel complet ;
- 3) la variation de la cadence d'émission des impulsions d'écholocation en fonction de la distance de l'animal à la cible au cours de la capture d'une proie immobile.

Ils permettent de faire des rapprochements avec les expériences faites dans le même esprit sur certaines Chauves-Souris, et devraient pouvoir servir de base à une meilleure connaissance des principes des sonars animaux en rendant possible des comparaisons ultérieures avec d'autres espèces.

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- RESUME -

On rapporte dans cette note les résultats d'une double étude expérimentale de l'écholocation chez Phocaena phocaena (L.).

L'une d'entre elles a montré que:

- 1° ces animaux, une fois aveuglés par des coupelles de caoutchouc, possèdent une capacité de détection d'obstacles filiformes qui est du même ordre de grandeur que lorsqu'ils utilisent pour cela leur système audio-visuel complet;
- 2° le seuil de détection par écholocation seule, dépend de la nature et de la forme géométrique des obstacles;
- 3° le seuil, déterminé par le diamètre des fils à 50 % d'évitement est de 0,2 mm. pour les fils métalliques, 0,8 mm. pour les fils de perlon torsadé 3 brins et 1 mm. pour les fils de nylon mono-brin. Ainsi, dans le cas des fils métalliques, le rapport entre la longueur d'onde de la composante maximale des signaux utilisés et le diamètre des fils est d'environ 3750.

La deuxième expérience a montré que lorsque les animaux s'approchent d'une cible alimentaire, ils le font en augmentant la cadence d'émission des impulsions d'écholocation tout au long de cette approche et que cette augmentation est telle que la courbe de la fréquence de répétition en fonction de la distance animal-cible est voisine d'une demi-courbe en cloche.

DISCUSSION

by

E. J. RISNESS

The experimental measurements reported here are extremely stimulating, since as well as answering many questions about the dolphin's method of detecting targets and avoiding obstacles, they provide much food for thought and raise some interesting possibilities.

One important question posed here, is the role of the dolphin's pulse repetition frequency in detecting and identifying targets or obstacles. In ship's sonar systems it is, for technical reasons, usually impracticable to listen at the same time as transmitting, and hence the pulse length and repetition interval are settled by the minimum and maximum ranges respectively in which the target might lie. But in the case of the dolphin it is pointed out that, at close range at least, the transmitted pulse and echo overlap. (The same is true with some bats, as pointed out by Dr. Griffin). If the animal can cope with this situation, why does it not transmit for longer, or more frequently? One possible reason is confusion between echoes at different ranges (adjacent if the pulse were longer, widely separated if the repetition frequency were higher). On the other hand it appears that the dolphin can easily resolve echoes spaced less than 1 metre (corresponding to a 1.2 m/sec pulse length), indicating that

its resolving power is determined by the bandwidth used rather than the pulse length. It would therefore appear that the answer to this question may lie in the physiology of the dolphin rather than the physics of the situation, e.g. a "time delay" in the dolphin's nervous system as suggested in the paper.

The role of bearing, as distinct from range, determination is not emphasized very strongly in these papers although, as several people have pointed out, the solution to a pursuit or an evasion problem can depend more critically on bearing than on range information. Some range information can be derived by measuring difference in bearing between spaced receivers - is it possible that the bat or the dolphin uses this technique?

There is a further possibility that the bearing of a target may be deduced using not only the direct echo from the target, but also the way in which the target modifies the ambient reverberation field. For example, the target can produce a "shadow zone" behind itself so that reverberation coming from this area is reduced. This effect has been observed with object lying on the sea-bed, where the absence of sound scattered back from the area behind the object is more detectable than the echo from the object itself. Is it possible that such effects are also used by bats or dolphins? One result of this would be that the useful information is received after the direct echo. Thus the received signal might no longer overlap with the transmitted signal, so avoiding other difficulties raised by this explanation, and also help to explain (on physical rather than physiological grounds) why the pulse repetition interval is

longer than would appear necessary.

Yet another possibility is that the dolphin does not use echoes directly from objects at short range, but continues to orient himself relative to such nearby objects using echoes from distant objects whose position relative to the nearby object he has previously fixed when he was further away. Again this would avoid the problem of transmit/receive overlap. Are we perhaps underestimating the importance of the animal's memory in relating current observations to past history?

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INTERPRÉTATION THÉORIQUE DE CERTAINES DONNÉES EXPÉRIMENTALES SUR L'ÉCHOLOCATION

par
Alon A. DZIEDZIC

INTRODUCTION

Dans une note précédente, Busnel et Dziedzic ont montré (1) que le Phocaena phocaena, en s'approchant d'une cible alimentaire expérimentale, émet des impulsions d'échololocation dont, en général, la fréquence de répétition varie en fonction de la distance et jusqu'à la prise de la proie, comme une demi-courbe en cloche.

Des tracés analogues ont, dans certains cas, été obtenus sur les chauves-souris par Griffin et ses collaborateurs (8, 9). Il semble d'ailleurs, que chez tous les animaux qui utilisent l'échololocation, il existe, entre la fréquence de répétition et le rapprochement de la cible, une relation croissante, généralement non linéaire, qui dépend de l'espèce ainsi que de certains paramètres spatio-temporels, liés à la nature de l'approche.

Il faut noter que durant ces approches, le comportement du Phocaena, en captivité depuis plusieurs mois, était très stéréotypé; l'animal décrivait en effet un circuit invariable dans le sens des aiguilles d'une montre, prenait sa respiration en un point fixe distant d'environ deux mètres de la cible, et terminait le parcours sous l'eau, d'une manière pratiquement rectiligne et uniforme.

Dans ces conditions, si l'on admet comme cela semble probable, que les enregistrements effectués correspondent bien à des signaux de localisation de la cible jusqu'à sa capture, on peut penser que l'allure de la courbe représentative de la fréquence de répétition des impulsions en fonction de la distance, doit être une caractéristique importante du processus d'échololocation.

Laboratoire de Physiologie Acoustique I.N.R.A., 78, Jouy-en-Josas, France.
R. G. BUSNEL, Directeur.

Travaux réalisés avec l'aide de l'I.N.R.A., du C.N.R.S., de la D.R.M.E. (Contrat n° 64-34092-00480-75-01), de l'O.T.A.N., de l'O.N.R. (Contrat n° 62555-3637) et de l'Université de Copenhague.

En se basant sur les résultats rapportés précédemment on tente ici, de donner une interprétation théorique de ces courbes, en tenant compte d'une part, des théories explicatives actuelles de l'évaluation des distances par écholocation, d'autre part, des caractéristiques physiques des signaux d'écholocation utilisés par Phocaena et qui ont déjà été décrits par ailleurs (2), et enfin des propriétés neurophysiologiques, anatomiques et sensorielles de l'animal qui entrent en jeu dans le processus d'écholocation.

A. Aspects physiques généraux des signaux d'écholocation

Si l'on considère l'étude analytique des signaux d'écholocation qu'émettent divers individus d'une même espèce animal, on remarque que les résultats concordent généralement bien, et que, les variations interindividuelles de structure et de forme sont faibles, mais que par contre, les résultats divergent grandement d'une espèce à l'autre et ce, au sein d'une seule et même famille zoologique.

Ainsi, dans le cas des Chauves-Souris de la famille des Vespertilionidae, les signaux de Myotis lucifugus ont une durée moyenne de 2,3 ms., et une fréquence composante qui décroît régulièrement de 78 à 39 kHz, tandis que Eptesicus fuscus émet des impulsions légèrement plus longues (2,7 ms.) modulées en fréquence comme celle de Myotis, mais entre 50 et 25 kHz seulement (8-18).

Chez les Rhinolophes, les signaux ont une durée nettement plus longue pouvant dépasser 30 ms., pour R. rouxi rouxi par exemple, mais de fréquence composante pratiquement constante, de l'ordre de 60 kHz (18).

Dans le cas des animaux marins et en particulier chez les Delphinidae, des différences interspécifiques existent également, mais elles résident plus dans les compositions spectrales des impulsions que dans leur durée: elle est par exemple du même ordre de grandeur (1 à 3 ms.) chez Phocaena et Tursiops, mais la composante de fréquence maximale est nettement plus basse chez le premier (2 kHz) que chez le second (20 kHz).

Ainsi donc, du fait de cette grande diversité dans les signaux utilisés par les différentes espèces animales, des propriétés physiques anatomiques et physiologiques qui leur sont propres, doivent régir le fonctionnement de leur système d'écholocalisation.

B. Importance de la distribution de la fréquence de répétition des impulsions chez *Phocaena phocaena* considérée du point de vue de deux des théories de l'écholocalisation

Parmi les différentes théories actuelles de l'écholocalisation, telles celles de Nordmark (16), Strother (23), Hartridge (13) ou celle enfin de Pye (20-21) et Kay (15), les deux dernières semblent apporter une explication valable du processus de discrimination de la distance animal-cible par certaines espèces de Chauves-Souris.

La théorie de Hartridge est fondée sur la perception par l'animal de l'intervalle de temps qui sépare l'émission et la réception de chaque impulsion, lequel est directement proportionnel à la distance animal-cible. Hartridge suppose qu'une contraction des muscles de l'oreille moyenne se produit en synchronisme avec les émissions, dont le niveau de perception serait alors fortement atténué.

La théorie proposée simultanément et indépendamment par Pye et par Kay attribue une importance primordiale à la modulation en fréquence des impulsions, émises par certaines Chauves-Souris comme les Vespertilionidae, et suppose que la perception de la distance par ces animaux repose sur un phénomène de battement qui se produit, lorsque l'émission et la réception de l'écho se superposent, au niveau de l'oreille externe de l'animal. Cette superposition, qui dépend de la durée de parcours de l'onde acoustique, entre le moment de son émission et celui de sa réception après réflexion, engendre une note de battement qui serait seule perçue par l'animal, et dont la hauteur lui apporterait l'information requise.

Il nous a semblé intéressant de confronter ces deux théories aux résultats expérimentaux obtenus sur *Phocaena phocaena* et de rechercher dans chaque cas une explication plausible des courbes expérimentales de la distribution des fréquences de

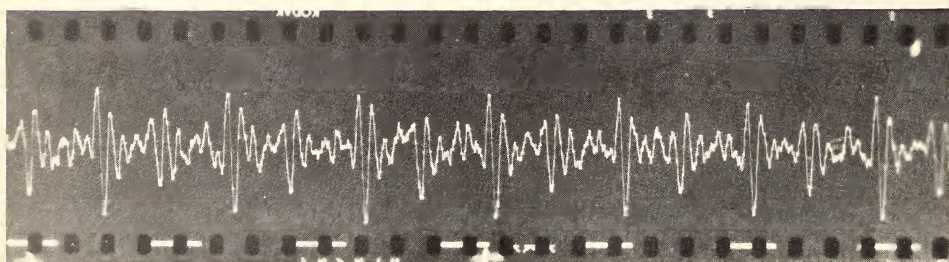
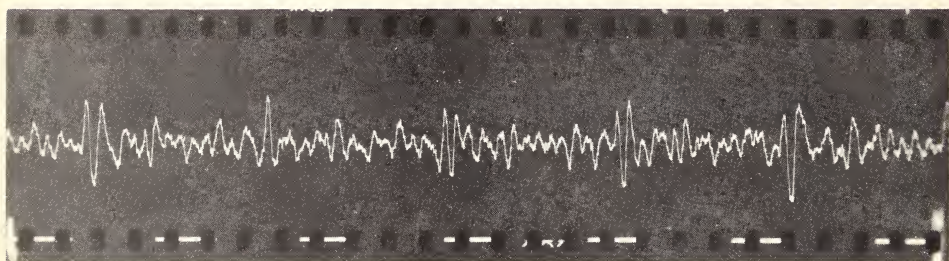
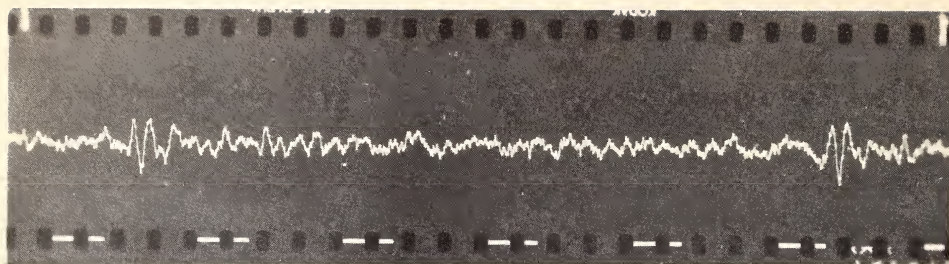


Fig. - : Oscillogrammes des impulsions d'écholocalisation
 émises par Phocaena phocaena lors de l'approche
 d'une cible alimentaire.
 En haut : distance animal-cible de 40 cm. environ.
 Au milieu : " " " " 20 cm. environ.
 En bas : " " " " 10 cm. environ.
 Base de temps : 3 cm. = 0,01 sec.

répétition des impulsions lors de l'approche des proies.

a. Application de la théorie de Pye et de Kay

Comme il a été rapporté plus haut, le Phocaena phocaena ainsi que d'autres Delphinidae, émet des impulsions d'écholocation dont la durée peut varier entre 1 et 3 ms., selon que l'animal se trouve plus ou moins rapproché de la cible. On a pu d'autre part observer, qu'à partir d'une distance relativement faible, de l'ordre de 60 cm. environ, la durée des signaux demeurerait pratiquement constante, étant dans la majorité des cas, de l'ordre de 1,2 ms. environ. La Fig. 1 représente les oscillogrammes d'une telle émission pour 3 distances différentes de l'animal lors d'une seule approche.

Si l'on considère alors, qu'en 1,2 ms. la partie frontale de l'impulsion parcourt, dans l'eau, une distance approximative de 1,80 m., cette partie parviendra à l'émetteur à l'instant où l'émission prendra fin, lorsque l'onde initiale aura rencontré un obstacle réfléchissant qui sera situé à 90 cm. de l'émetteur. Mais, comme au-delà de 60 cm. les impulsions sont généralement plus longues, c'est donc à une distance supérieure que la superposition se produit, en particulier, elle se fera déjà à une distance de 2,25 m. pour les impulsions de 3 ms.

Toutefois, étant donné, d'une part, que chez les Delphinidae, on ne constate aucune variation régulière de la fréquence composante des impulsions, contrairement à ce qui s'observe chez les chauves-souris de la famille des Vespertilionidae, et comme en outre, la distribution spectrale de ces impulsions s'apparente plus à un phénomène transitoire à spectre de bruit (19) qu'à celui d'un spectre ordonné, et que d'autre part, chez Phocaena en particulier, une impulsion de 1,2 ms. ne comporte que 2,4 périodes à la fréquence d'intensité maximale (2 kHz), il semble très improbable qu'un battement puisse dans ces conditions être le facteur de perception par écholocation, de la distance des cibles, comme le suggère la théorie de Pye et de Kay.

b. Application de la théorie de Hartridge

Cette théorie implique que le rythme des influx dans le

système nerveux auditif, suivie en synchronisme celui des stimulations acoustiques externes, qui sont interprêtées ensuite dans le système nerveux central.

Dans ce cas la période réfractaire de l'ensemble des éléments nerveux doit être plus brève que l'intervalle minimum entre 2 stimuli successifs, qui dans le cas du Phocaena est de l'ordre de 1,36 ms. pour la fréquence maximale de répétition observée (736 impulsions par seconde).

Les caractéristiques physiologiques du système nerveux auditif des mammifères marins sont encore peu connues, mais les nombreux résultats électrophysiologiques obtenus sur d'autres espèces utilisant l'écholocation permettent, comparativement, de supposer qu'il est susceptible de satisfaire à cette exigence (10-14).

Toutefois, contrairement à la théorie de Pye, celle de Hartridge ne peut s'appliquer que dans les cas où la superposition entre l'impulsion directe et l'écho n'a pas lieu au niveau du récepteur puisqu'alors, la distinction des intervalles de temps serait impossible; or, il a été montré plus haut que cette superposition peut avoir lieu lorsque la distance animal-cible est inférieure à 2,25 m. Par ailleurs, une contraction synchrone avec les émissions, des muscles de l'oreille moyenne des Delphinidae, devrait alors s'effectuer avec une rapidité jamais observée chez les mammifères; on doit donc admettre que la théorie de Hartridge est difficilement applicable à ces animaux.

C. Essai d'interprétation du mécanisme de l'écholocation chez Phocaena phocaena à partir des courbes expérimentales

L'analyse physique des signaux d'écholocation de Phocaena rapportée plus haut, conduit donc à rejeter l'éventuelle possibilité d'application des deux principales théories de la détermination acoustique de la distance des cibles qui ont été émises pour certaines espèces de chauves-souris. Il convient donc de voir maintenant s'il est possible de donner une explication du fonctionnement du système d'écholocation du Phocaena qui puisse satisfaire aussi bien aux propriétés neurophysiologiques, sensorielles et anatomiques de l'animal, qu'aux résultats observés de l'analyse physique.

a. Aspect neurophysiologique

Nombreux sont les travaux d'électrophysiologie réalisés sur l'audition des Chauves-Souris; les plus importants dans le domaine qui nous intéresse ici, étant actuellement ceux de Grinnell sur Myotis lucifugus et Plecotus townsendii (10-11-12) et de Friend et ses collaborateurs (6) sur le même Myotis lucifugus.

D'après Grinnell, ces animaux semblent posséder des caractéristiques neurophysiologiques spécialement bien adaptées à la perception et à l'analyse individuelle de stimuli acoustiques très brefs, répétés à cadence élevée. En particulier, cet auteur trouve que la période réfractaire des neurones des voies auditives de la Chauve-Souris, consécutive à une stimulation intense, serait beaucoup moins grande que celle observée chez d'autres Mammifères comme l'Homme, le Chat ou le Cobaye. Ainsi, il semblerait que dans le cas de deux stimuli consécutifs, séparés de 1 à 2 ms. seulement, les potentiels évoqués respectifs, au niveau du tubercule quadrijumeau postérieur, soient nettement différenciés.

On peut donc admettre que la période réfractaire des voies auditives de la Chauve-Souris est extrêmement brève, ce qui les rend aptes à percevoir individuellement des stimuli acoustiques répétés à cadence élevée.

Comme les expériences sur la discrimination des obstacles par Phocaena montrent (1) que l'acuité de leur système d'écholocation est au moins aussi grande que celle des Chauves-Souris, pour des fréquences de répétition, beaucoup plus élevées, on peut supposer que la spécialisation de leur système auditif doit être très grande et qu'il doit posséder également des caractéristiques physiologiques qui l'adaptent à la transmission rapide des influx nerveux, et à la perception individuelle de chaque écho.

b. Aspect anatomique

Dans sa théorie précédemment rappelée, Hartridge admet que chez

les chauves-souris, les muscles de l'oreille moyenne se contractent lors de l'émission de chaque impulsion d'écholocation, afin de réduire la perception de leur intensité et éviter l'inhibition du système nerveux auditif par ces stimulations directes.

Si un tel phénomène neuromusculaire peut être envisagé, et a même été démontré, chez les animaux qui perçoivent des stimulations auditives à un rythme relativement lent, il ne l'est plus chez les Delphinidae qui répètent et reçoivent leurs émissions plusieurs centaines de fois par seconde, car une telle rapidité de réponse musculaire n'a été observé chez aucun Mammifère. Par contre, une des caractéristiques du système nerveux de ces animaux étant précisément ce phénomène inhibiteur temporaire produit par les stimulations intenses, les Delphinidae doivent également y être sujets, mais alors des propriétés particulières autres que les contractions synchrones doivent intervenir pour soustraire ces animaux à cet assourdissement temporaire.

La manière dont le système auditif des Delphinidae est protégé contre les émissions directes très intenses n'est pas connue avec précision. Néanmoins, d'une part, certains travaux anatomiques de Reysenbach de Han (23) et de Fraser et Purves (5) montrent que l'oreille interne de ces animaux est extrêmement bien isolée dans la cavité crânienne et que la transmission acoustique par conduction interne depuis l'organe émetteur jusqu'à la cochlée est extrêmement faible (inférieure à 3 %); d'autre part le récent travail de Norris et Evans (17) sur Tursiops truncatus met en évidence que l'émission des signaux d'écholocation chez cet animal est très directive, de sorte que les conduits auditifs externes semblent être situés en dehors de leur diagramme de directivité le plus large.

Si donc on attribue au Phocaena les résultats obtenus par ces différents chercheurs sur d'autres Delphinidae, on voit que lors de l'écholocation, l'animal ne perçoit pratiquement pas son émission par conduction osseuse ou tissulaire, ni par transmission acoustique externe et que par suite de

cette morphologie anatomique particulière et de la position des organes auditifs périphériques en dehors du diagramme de directivité de l'émission, le système auditif de l'animal est beaucoup plus réceptif aux bruits extérieurs qu'à son émission propre. Il convient de souligner qu'une telle hypothèse implique uniquement que l'animal ne perçoit pas auditivement son émission, dont il peut par ailleurs avoir "conscience" par une sensation proprioceptive.

S'il en est bien aussi, seuls les échos des émissions doivent alors intervenir dans le processus d'écholocation utilisé par les Delphinidae et, dans ce cas, l'information de la distance animal-cible doit être donnée par la comparaison des intervalles de temps entre les échos successifs, chaque émission étant déclenchée par la réception de l'écho précédent.

D. Développement mathématique

En partant d'une telle hypothèse on a cherché à déterminer la distribution théorique des impulsions successives lorsque l'animal s'approche linéairement et à vitesse constante v d'une cible.

On a tenu compte tout d'abord d'un facteur temporel global τ , qui dépend uniquement de l'animal, et pendant lequel ont lieu les processus neuromusculaires concernant l'émission du signal, et neurophysiologiques, concernant l'audition depuis la périphérie jusqu'à l'analyse centrale; ensuite des facteurs physiques relatifs à la propagation des signaux acoustiques depuis leur émission jusqu'à leur arrivée sur les organes externes de réception.

Ainsi en désignant par :

t_0 l'instant d'émission de la 1ère impulsion consécutive à la perception du premier écho,

d_0 la distance animal-cible correspondant à t_0 ,

t_n et d_n respectivement l'instant d'émission de la $n + 1$ ème

impulsion et la distance correspondante animal-cible,

par Δt_n l'intervalle de temps entre la $n - 1$ éme et la n éme émission,

par V la vitesse de propagation des ondes acoustiques dans le milieu ambiant et par α le rapport:

$$\frac{V-v}{V+v} ;$$

la distribution des distances animal-cible à chaque émission sera:

$$d_1 = d_o \alpha - v \tau$$

$$d_2 = d_o \alpha^2 - v \tau \alpha - v \tau$$

$$d_n = d_o \alpha^n - v \tau (\alpha^{n-1} + \alpha^{n-2} + \dots + \alpha + 1)$$

Soit:

$$d_n = d_o \alpha^n - v \tau \frac{1 - \alpha^n}{1 - \alpha}$$

tandis que la distribution correspondante des Δt sera:

$$\Delta t_1 = \frac{2d_o}{V+v} + \tau$$

$$\Delta t_2 = \frac{2}{V+v} (d_o \alpha - v \tau) + \tau$$

$$\Delta t_n = \frac{2}{V+v} (d_o \alpha^{n-1} - v \tau \alpha^{n-2} - \dots - v \tau) + \tau$$

Soit:

$$\Delta t_n = \frac{2}{V+v} \left[d_o \alpha^{n-1} - v \tau \frac{1 - \alpha^{n-1}}{1 - \alpha} \right] + \tau$$

ou encore:

$$\Delta t_n = \alpha^{n-1} \left(\frac{2d_o}{V+v} + \tau \right)$$

D'où l'on tire la distribution des intervalles Δt_n en fonction des positions correspondantes d_n de l'animal:

$$\Delta t_n = \frac{1}{\alpha} \left(\frac{2d_n}{V+v} + \tau \right) \quad (1)$$

En pratique, dans le cas de l'écholocation, on pourra prendre α égale à l'unité, puisque V est toujours très supérieur à v , et Δt_n en fonction de d_n , sera exprimée par la somme des deux fonctions l'une physique $\frac{2d_n}{V+v}$, l'autre physiologique τ .

a. Importance relative de $\frac{2d_n}{V+v}$ et de τ dans les courbes expérimentales obtenues sur *Phocaena*

Si l'on applique la formule précédante aux résultats expérimentaux obtenus avec *Phocaena* on constate que:

- 1° $\frac{2d_n}{V+v}$ varie comme une droite en fonction du temps, et que sa valeur est pratiquement indépendante de la vitesse d'approche v négligeable devant V .
- 2° La forme des courbes expérimentales ne peut s'expliquer que si l'on admet que τ est variable.
- 3° C'est précisément τ qui est prépondérant dans la valeur de Δt_n et limite la fréquence de répétition qui ne peut dépasser la valeur $\frac{1}{\tau}$.
- 4° A courte distance l'écholocation semble alors relever beaucoup plus de la physiologie que des conditions physiques de transmission des ondes.

A titre indicatif, pour $d_n = 50$ cm, $\frac{2d_n}{V} = 0,67$ ms. dans l'eau, alors que la valeur expérimentale moyenne correspondante de Δt_n est environ 10 ms. que l'on doit attribuer en majeure partie à τ .

b. Interprétation de la fonction τ

On vient de voir, que l'hypothèse envisagée, selon laquelle dans l'écholocation, l'animal ne perçoit auditivement que les échos et non son émission propre, conduit à admettre que l'allure générale des courbes expérimentales obtenues sur Phocaena, dépend en premier lieu de ses propriétés psychophysiques et neurologiques. Il convient donc de rechercher maintenant si, chez les Mammifères, ces facteurs sont effectivement soumis à des variations analogues en fonction de la cadence des stimulations.

L'aspect neurophysiologique du problème de l'écholocation abordé plus haut a montré que, les stimuli individuels se succédant à des intervalles de temps de l'ordre de 1 à 2 ms., c'est à dire, répétés 500 à 1000 fois par seconde, provoquent, au moins chez certaines chauves-souris, des réponses neurales distinctes. Il ne paraît donc pas absurde d'admettre que chez Phocaena, la transmission des influx nerveux, peut également suivre la fréquence maximale de répétition observée, comprise entre 500 et 700 impulsions par seconde.

Par ailleurs, de nombreux travaux électrophysiologiques sur les Mammifères (3, 4, 7) ont mis en évidence que le temps d'apparition des réponses neurales est, en un point donné du système nerveux, d'autant plus important que la fréquence de répétition et l'intensité des stimulations sont grandes. Si l'on admet alors, qu'il en est de même chez Phocaena, on peut donc attribuer en grande partie, la limitation progressive de l'accroissement de la fréquence de répétition, à l'augmentation du temps de latence du système nerveux auditif de l'animal.

Les considérations précédentes ne tiennent compte que des propriétés physiques et neurologiques qui entrent en jeu dans la discrimination de la distance d'une cible par écholocation. Il convient d'examiner maintenant de quelle manière les lois psychophysiques classiques pouvaient s'appliquer aux phénomènes observés.

En abordant alors le problème de ce point de vue, il est

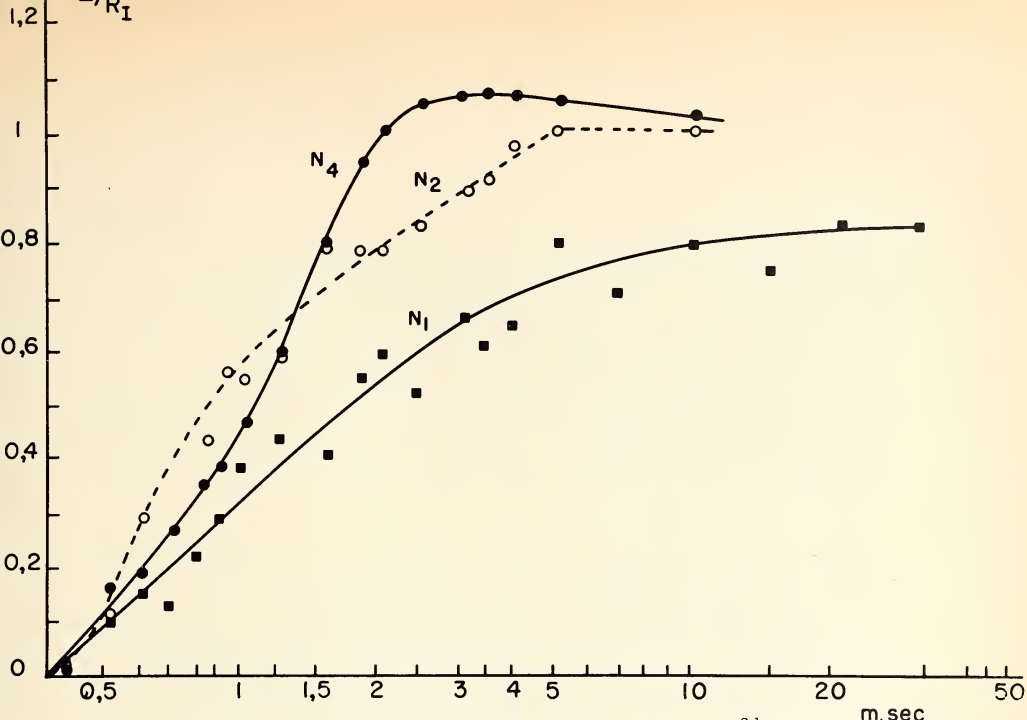


Fig. 2 : Importance respective du terme physique $\frac{2d}{v}$ et du terme neurophysiologique τ , dans la répartition expérimentale des intervalles de temps entre impulsions successives, émises par Phocaena lors de l'approche d'une cible alimentaire.

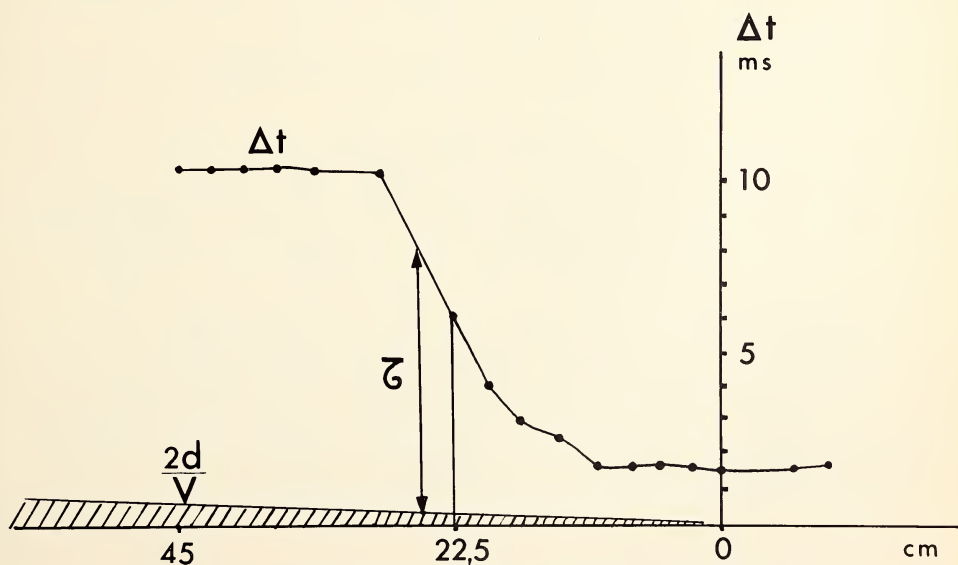


Fig. 3 : Distribution types de la fréquence de répétition des impulsions d'écholocation émises par deux Phocaena, lors de l'approche d'une cible alimentaire.

- a. Fréquence de répétition (F.R.) en échelle linéaire (ordonné)
Temps précédant la prise de la proie en s. (abscisse)
- b. Fréquence de répétition (F.R.) en échelle logarithmique (ordonné).
Temps précédant la prise de la proie en s. (abscisse)

possible de montrer que la courbe expérimentale de variation de la fréquence de répétition des signaux, obtenue chez Phocaena, peut trouver son explication dans la loi générale de Weber-Fechner. Cette loi qui exprime en effet, que l'augmentation de la sensation est plus lente que celle du stimulus, et qu'il y a un certain retard entre effet et cause "dans le processus de transformation de l'énergie de la sphère physique à la sphère psychique", (24) est applicable à tous les domaines sensoriels, et en particulier dans celui de l'audition, à la reconnaissance subjective de la hauteur des sons.

Si donc, dans le processus d'écholocation on considère qu'il existe une fonction de corrélation entre les intervalles des impulsions successives et l'éloignement de la cible ou, ce qui revient au même, que cadence de répétition et proximités sont liées par une fonction caractéristique, la perception subjective du rapprochement de cette cible, sera déterminée par l'application de la loi de Weber-Fechner à cette fonction.

c. Conséquence de l'application de la loi de Weber-Fechner à l'écholocation des proies par Phocaena

Si l'on reporte sur une échelle logarithmique la fréquence instantanée de répétition des impulsions en fonction de la distance, lors des approches des proies par Phocaena, on constate que dans de nombreux cas, la partie de la courbe comprise entre le point de localisation L et le point de décision C, peut être assimilée à une droite (Fig. 3), et que par conséquent, entre ces deux points, la fréquence de répétition peut être considérée comme une fonction exponentielle de la distance, quand ces approches sont linéaires et uniformes. Si l'on applique alors la loi logarithmique de Weber-Fechner à cette portion de courbe, la perception subjective de la distance de la cible sera alors inversement proportionnelle à la fréquence. On pourrait penser alors que cette variation exponentielle de la fréquence de répétition, qui compense en quelque sorte la loi logarithmique de Weber-Fechner, permet à l'animal d'estimer la distance dans l'échelle linéaire, comme le temps ou la vitesse d'approche.

REMARQUES

En dehors de certaines limites indiquées par les points L et C de la courbe expérimentale, la loi de Weber-Fechner n'apporte plus sa justification à la distribution de la fréquence de répétition des impulsions, mais il est bien connu que cette loi n'est pas applicable pour des valeurs extrêmes des stimuli et les courbes expérimentales en deçà du point L et au delà du point C, peuvent éventuellement admettre l'explication intuitive donnée dans la note précédente (1).

CONCLUSIONS

L'explication du mécanisme de la perception des distances par écholocation chez les Delphinidae, proposée ici, modifie certains aspects de la théorie de Hartridge. Il repose d'une part, sur des données neurophysiologiques acquises chez d'autres Mammifères qui utilisent un système analogue, d'autre part, sur l'anatomie de l'organe auditif des Dauphins et enfin, sur des résultats expérimentaux obtenus sur Phocaena phocaena. En outre, cette théorie semble être en accord avec les lois psychophysiques dont l'intervention ne peut être ignorée dans l'étude de tous les phénomènes sensoriels.

En abordant le problème de ces différents points de vue, il semble donc que:

1. La forme des courbes expérimentales de la fréquence de répétition des impulsions lors de l'approche d'une cible, dépend plus, à courte distance, des capacités neurophysiologiques du système auditif de l'animal que les lois de la propagation des signaux dans le milieu ambiant.

2. Par suite du retard entre la sensation au niveau de la sphère sensorielle du cortex et la stimulation extérieure (où la loi psychophysique de Weber-Fechner semble trouver son explication), la distribution particulière de la fréquence de répétition permet au Phocaena d'estimer la distance de la cible par la perception de cette fréquence de répétition; distance et fréquence perçues étant alors inver-

sement proportionnelles.

Cette théorie semble donc apporter une explication vraisemblable des résultats expérimentaux obtenus sur la perception de la distance des cibles par Phocaena. Elle ne modifie pas les idées relatives à la localisation spatiale des cibles par perception binaurale, et à la reconnaissance de leur nature par la composition spectrale des échos.

REMERCIEMENTS

L'auteur tient à remercier vivement le Dr. L. Pimonow, le Dr. J.P.Legoux et l'I.G.M. Levy des nombreuses suggestions et critiques qu'ils lui ont apportées au cours de ce travail.

- RESUME -

On étudie ici, d'abord l'importance de la distribution de la fréquence de répétition des impulsions d'écholocalisation en fonction de la distance animal-cible, observée par ailleurs (1) sur Phocaena phocaena (L.), dans son application aux diverses théories connues de l'écholocalisation.

On montre ensuite que si l'on admet que les Delphinidae n'ont qu'une perception proprioceptive de leur émission directe et s'ils ne perçoivent auditivement que les ondes réfléchies, la distribution trouvée dépendra plus, à courte distance, des capacités neurophysiologiques du système auditif de l'animal que des lois de la propagation des signaux, ce qui par suite de la loi de Weber Fechner lui permettrait d'estimer la distance des obstacles par la cadence de réception des échos.

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DISCUSSION

par

L. GERARDIN

Les communications en question contiennent de très nombreux résultats expérimentaux sur les problèmes de discrimination d'objectifs, tant par les chauves-souris que par les dauphins. Il serait intéressant d'écrire le bilan de transmission de la liaison, compte tenu des surfaces d'écho des objectifs (il faut noter sur ce dernier point qu'un fil très fin, mais de grande dimension longitudinale, donne un écho important). Donc de voir si effectivement le rapport signal sur bruit qui assure la détection à 50% de chances et 1 % de fausse alarme est d'environ 7 décibels par impulsion.

Le matériel expérimental résumé dans les figures 1 et 2 de l'étude b) devrait permettre de comparer la courbe probabilité de détection en fonction du rapport signal sur bruit avec ce que prévoit la théorie classique du signal.

L'établissement de ce bilan de transmission suppose connues toutes les données du problème et c'est pourquoi je laisse aux biologistes le soin de l'écrire. Tant qu'il n'aura pas été écrit en détail, on doit réserver son jugement sur l'hypothèse é-

noncée à la page 6 de a) "the bats detected wires ... more successfully than is possible even for the ideal detector of signal detection theory !". En fait, un paramètre mal connu est celui de la bande passante effective du récepteur des sonars biologiques. Les études physiologiques de Alan D. GRINNEL sont extrêmement précieuses à cet égard, en suggérant l'hypothèse d'une bande étroite de réception. Mais y a-t-il en outre réduction ultérieure de bande (ou non) par intégration de plusieurs impulsions, la chiffraison aussi précise que possible du bilan de transmission apporterait un élément de réponse dans ce débat.

Quelle est l'information de base détectée par un sonar biologique ? Il semble évident de répondre la distance, à l'image des matériels radars ou sonars. La modulation de fréquence suggère même qu'il y aurait compression d'impulsion. En fait, si l'on examine le problème sans idée a priori, il est évident que la connaissance très précise de la distance ne sert strictement à rien. Par contre, pour que la poursuite d'une proie soit couronnée de succès, il est essentiel de savoir dans quelle direction est située cette proie. L'information de base est donc celle de direction angulaire et non celle de distance. Comme la vitesse de l'animal intercepteur (chauve-souris ou dauphin) est nettement supérieure à celle de l'animal intercepté (moucheron ou poisson), l'étude cinématique et dynamique de l'interception montre que la seule information nécessaire est la direction angulaire de l'intercepté vue de l'intercepteur. Un engin autoguidé comme le Hawk ne fonctionne pas autrement.

Il est dommage que rien ne soit dit sur ce sujet et la question est donc à poser aux biologistes : comment l'animal é-

value-t-il gisement et site. Il a deux oreilles, certes, et ceci lui permet de faire une localisation monopulse dans un plan, celui de gisement. Mais le site ? D. CAHLANDER a imaginé que l'oreille des Vespertilionidés, grande vis-à-vis des longueurs d'ondes ultrasonores, était dispersive en fréquence, ce qui permettrait à l'animal d'évaluer les directions site par l'analyse des fréquences reçues. Ayant discuté de ce problème avec Dorothy C. DUNNING, cette dernière m'a fait remarquer que l'oreille réelle d'un animal n'avait pas la perfection d'un réflecteur en métal et qu'il y avait donc lieu d'interpréter avec prudence.

Dans le cas des Rhinolophidés, l'évaluation du site pourrait avoir lieu grâce au mouvement d'exploration rapide et de grande amplitude des oreilles. On a parfois parlé de modulation Doppler au sujet de ce mouvement, mais il est très peu probable que les récepteurs animaux soient capables d'évaluer un battement Doppler. En effet, qui dit Doppler entre deux signaux, sous entend que ces signaux sont à fréquence pure ; en d'autres termes, lorsque l'émission a lieu par impulsions, il faut qu'il y ait cohérence de phase d'une impulsion à la suivante, cohérence liée à l'existence d'un oscillateur continu de référence. Cette cohérence de phase est une des difficultés technologiques principales des radars dits pulse-doppler. On ne voit pas très bien comment les émetteurs biologiques pourraient l'assurer. Or, en l'absence de cette cohérence, il n'y a plus de Doppler, mais juste une sorte de bruit inexploitable. Le mouvement des oreilles des Rhinolophidés est donc beaucoup plus probablement à rattacher à ce problème de mesure angulaire qu'à celui de détection proprement dit. La question est ouverte, les observations des biologistes devraient permettre de la faire progresser.

A la lecture des études présentées, l'ingénieur ne peut manquer d'être frappé par l'extraordinaire faculté d'identification montrée par les sonars animaux . En particulier par les résultats rapportés par D.R. GRIFFIN , J.H. FRIEND et F.A. WEBSTER (J. of Exp. Zool. March 1965) sur la discrimination entre des asticots et des petits disques métalliques. La discrimination entre des sphères (échos d'intensité constante) et des asticots (échos d'intensité fluctuante à fluctuations rapides : ordre du dixième de seconde) s'explique plus aisément.

Ce qui serait intéressant à connaître , c'est le nombre exact de Myotis qui passèrent les tests et quelle fut l'allure de la courbe d'apprentissage (dans le cas asticots-disques). La discrimination a lieu à longue distance puisque, comme le montre la figure 1, les disques ne sont généralement pas poursuivis. Il est difficile de voir à première vue, d'après l'analyse des figures 2 et 3 du même article, en quoi diffère la réponse fine en fréquence des deux objets . La fréquence basse fréquence à laquelle avait lieu la modulation d'intensité des retours d'échos n'est pas indiquée (seule est mentionnée la variation de l'orientation d'un asticot de 90 degrés en un dixième de seconde).

Bien que l'on ait beaucoup écrit sur le processus de reconnaissance, de pattern recognition, il faut reconnaître honnêtement que le sujet est encore fort obscur. Quelle est la quantité d'information nécessaire pour faire la distinction entre un asticot et un petit disque de même diamètre moyen (ou entre un rond et un carré). Pour répondre à cette question, il faudrait savoir par quelles données de base se caractérise chaque catégorie. On a beaucoup écrit sur la phase classification, facilement mathématisable, très peu sur le phase préliminaire de transformation des données brutes en éléments élaborés capables de donner lieu à

classification. Le sujet a été abordé d'un point de vue philosophique dans l'essai de Kenneth M. SAYRE : Recognition : a study in the philosophy of artificial intelligence (University of Notre Dame, Press 1965). Les psychologues et les mathématiciens peuvent-ils apporter quelque lumière supplémentaire.

En résumé, que peut-on dire du bilan énergétique de la détection sonar biologique, comment les animaux localisent-ils angulairement leur cible, quelle est la quantité d'information nécessaire pour apprendre à accomplir une classification dichotomique.

201165

DISCRIMINATION
OF DIFFERENT METALLIC PLATES
BY AN ECHOLOCATING DELPHINID

by
W.E. EVANS and B.A. POWELL

INTRODUCTION

The echolocating capability of the Atlantic bottle-nose dolphin, *Tursiops truncatus*, (5) and Harbor porpoise, *Phocoena phocoena*, (1) has been well demonstrated by observing the ability of these animals to avoid obstacles and discriminate a preferred object from a non-preferred object while blindfolded. The signals produced by these species during echo ranging have also been recorded and analyzed. However, little control has been exercised over the acoustical properties of the targets and/or the location and orientation of the animal in either reference to the targets or the recording transducer. Without these data it is difficult to determine which parameter, or series of parameters, of the target echo provide information to the animal.

The purpose of this study was to determine the ability of a blindfolded delphinid, *Tursiops truncatus*, to discriminate between two targets which varied theoretically only in the intensity of the echo. In addition, the tests were designed so that the animal's sound emissions and location in relation to the targets and transducers could be monitored and recorded during each trial.

MATERIAL AND METHODS

Targets:

Desired targets were ones for which the effects on an incident broadband pulse could be estimated. Cylinders and spheres were not considered suitable since changes in diameter would not only change echo strength but also the frequency content of the reflected pulse. This would make the effect of changes in target reflectivity on discrimination difficult if not impossible to determine. In line with these considerations, metallic plates were chosen for targets. Copper, brass, and aluminum were selected as test materials because published data on their acoustic impedances were available (7). Since there is some known variation in the properties of available metals, the density of each material used was measured and the published values of acoustic impedance ($\rho_0 c_0$) corrected accordingly. Using the formulation presented in detail in Officer, 1958 (6) a computer program was prepared, and the reflectivities as a function of frequency in the range of 2kHz to 200 kHz were computed for a wide range of plate thicknesses. This range of frequencies was selected because it adequately covered the range of hearing sensitivity demonstrated for the Atlantic bottlenose dolphin, *Tursiops truncatus*, by Johnson (2).

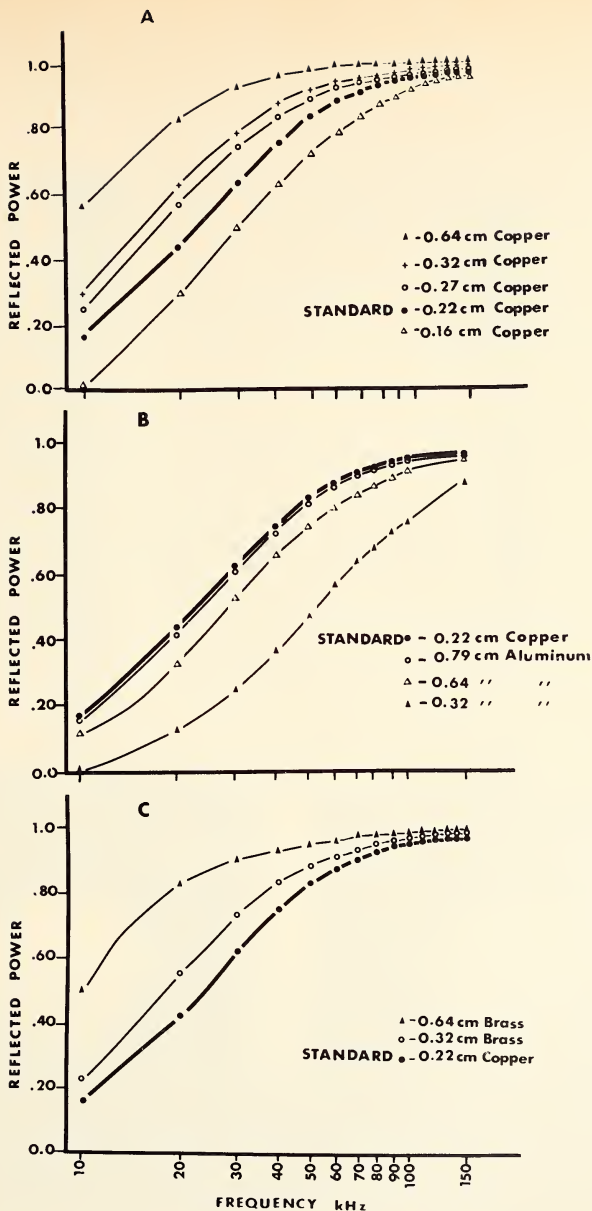


FIGURE CAPTIONS

Figure 1a-1c Reflected power as a function of frequency for the material selected as the standard target (0.22 cm thick copper) versus (a) 0.64 cm, 0.32cm, 0.27cm, and 0.16 cm copper, (b) 0.79 cm, 0.64 cm and 0.32 cm aluminum, and (c) 0.64 cm and 0.32 cm brass. The reflected power is the square of the amplitude (pressure). If reflected amplitude versus frequency were plotted the apparent separation between targets would be decreased considerably.

These initial computations were utilized in determining the thicknesses of each material to be used. Since the psycho-physical method of constant stimuli (8) was to be used, a standard target to which all other targets could be compared had to be selected. Using the preliminary data on reflectivity as a function of thickness, 0.22 cm thick copper was selected as the standard target. This thickness of copper represented an advantageous median thickness around which a wide range of comparison targets of different thicknesses and materials could be presented in more or less graduated steps of reflectivity. The reflectivity as a function of frequency for the copper, aluminum and brass plates selected for the test are compared to the 0.22 cm thick copper standard target in Fig. 1a - 1c.

All of the test plates, including the standard, were prepared as 30 cm diameter discs. The target holders were constructed of 0.32 cm brass, 30 cm by 30 cm by 2.54 cm and covered with 0.64 cm sponge neoprene. A 17.2 cm diameter circular window was cut in the center of each holder, and the targets were mounted from the back. Thus, the animal was presented with a 20 cm metal disc

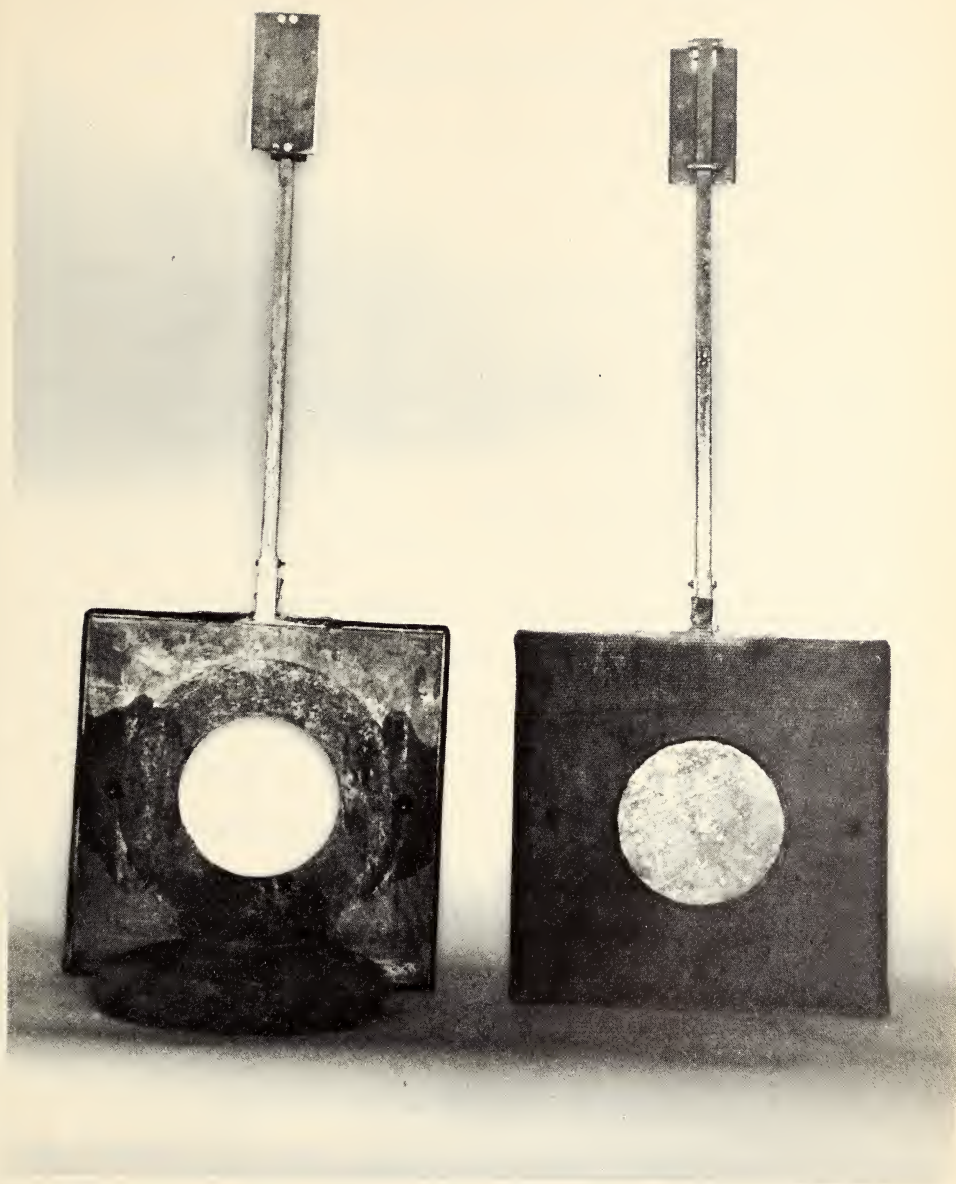


Figure 2 Front and rear views of the target holders and typical targets used in this study.

in the center of a 30 cm square neoprene background (fig. 2). The purpose of this mounting arrangement was to negate the possibility that the animal could scan on the edge of the test targets.

Test Procedures:

The tests were conducted in a circular concrete tank 9.14 meters in diameter and 1.22 meters deep. The experimental animal, a 148 kgm, female Atlantic bottlenose dolphin, *Tursiops truncatus*, was trained by standard operant conditioning techniques, to wear opaque silicon rubber cups over her eyes in a fashion similar to that described by Norris et al (5). Wearing the blindfolds the animal was then trained to station herself at one end of a 7 meter long, 1 meter wide, plywood runway laid on the bottom of the tank. When cued by a broadband pulse, she was to swim down the runway and select the standard target from the pair presented there. The animal indicated her choice by pressing the target with her rostrum. If the standard target was selected, she was reinforced with 3-4 surf smelt, *Hypomesus pretiosus*.

Two sets of standard and comparison targets were prepared: The target position (right or left); the target

holder; and surface of the target presented to the animal were all randomized. Test runs were conducted in the morning and afternoon for a total of 40 trials per day.

Data Collection:

A video camera was positioned 2.2 meters above the surface of the water and was focused to cover the last 2 meters of the runway and the target area. The output of this camera and that of a broadband hydrophone (100 hz - 110 kHz, \pm 2dB, Atlantic Research Corp. LC-32) were recorded on a Sony video tape recorder. The hydrophone was positioned directly between and parallel with the test targets with its acoustic center at the same depth as the center of the targets. This arrangement allowed the simultaneous recording of the animal's sonic emissions and her positioning during the last two meters of each trial.

The second audio channel of the Sony video recorder was used to record 10 per second 10kHz timing pulses. These timing pulses and the output of the hydrophone were also recorded on an Ampex FR 1300 magnetic tape recorder at a tape speed of 152.4 cm per second. This procedure allowed the recording of the full band width of the hydrophone (100Hz - 110 kHz) and the relating of this broadband acoustic data to the positional data recorded on the video recorder.

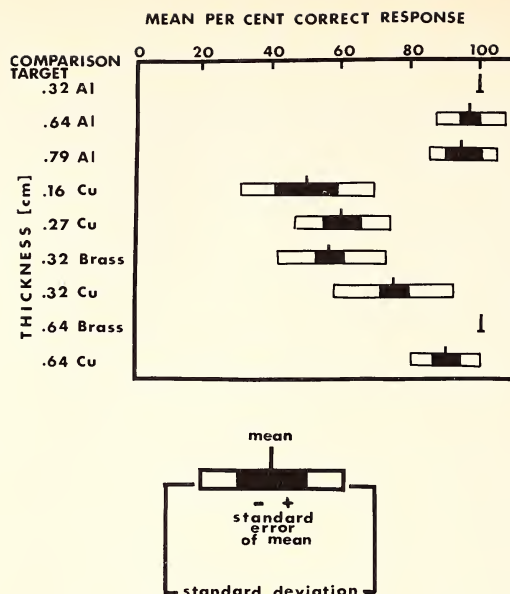


Figure 3

The mean percent correct response, \pm one standard deviation (SD) and one standard error of the mean, for all the targets tested. Cu refers to copper and Al refers to aluminum.

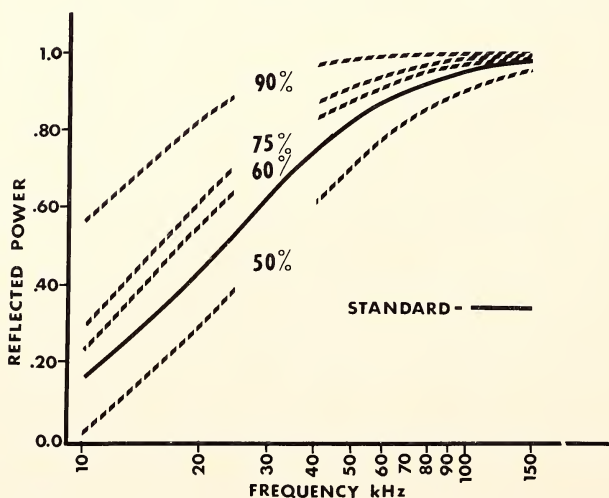


Figure 4

Reflected power versus frequency and associated performance scores for all the copper versus copper comparisons.

RESULTS

Limits of Discrimination:

The mean percent correct response, standard deviation, and standard error of the mean for all targets tested are presented in Fig. 3. These data indicate that the animal was unable to discriminate 0.32 cm brass, 0.27 cm copper, and 0.16 cm copper from the 0.22 cm copper standard.

In referring back to Figs. 1a - 1c it will be seen that the reflectivity of 0.27 cm copper and 0.32 cm brass are almost identical. Considering only copper versus copper comparisons, the ability to discriminate is severely limited at thicknesses of 0.05 cm above the standard and 0.06 cm below the standard of 0.22 cm. This represents a mean difference in reflectivity of +.04 and -.06. The reflected power versus frequency and the associated performance scores for all the copper targets tested are presented in Fig. 4.

In the comparison of aluminum targets to the standard target, all the performance scores were above the 90% level (Fig. 3). Even though the 0.79 cm aluminum target had a mean difference in reflectivity of 0.02, the mean performance was 95% correct responses. This would seem to indicate that information other than or in addition to

intensity of the echo was used by the animal. This paradox will be discussed in more detail later (See Johnson this volume).

Collateral Behavior:

In addition to the performance scores it was thought that other aspects of the animal's behavior might be indicative of the difficulty of the discrimination. Those considered were (1) the number of times the animal reoriented its head from one target to the other; (2) the total time it took the animal to traverse the last two meters of the run and select a target; and (3) the pulse repetition rate.

During the course of each test run, the blindfolded animal moved its head from side to side and up and down in scanning motions similar to those described by Norris et al (5) and Kellogg (3). By studying the video tapes of various test runs, it was apparent that in addition to these head scanning motions the animal reoriented her whole body and rolled from side to side.

Very little scanning took place during easy discriminations (performance scores greater than 90%). This "scanning rate" increased almost threefold for difficult discriminations (performance scores less than 60%).

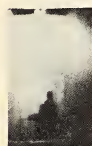
In this latter case it appeared as though the decision as to which target to push was made at less than one meter from the display. In easy discriminations the decision was made at distances greater than one meter from the target. These data are presented in Table I.

The mean time for the animal to swim the last two meters of the runway and select a target was 5.3 seconds for the easy discriminations and 7.1 seconds for the more difficult ones. This increased mean time for the difficult problem is not, however, indicative of a slower swimming speed. The animal's speed was essentially constant for easy and difficult discriminations to within one meter of the targets. The greater number of head reorientations at ranges less than one meter from the plates for the difficult comparisons can account for the increased time in the target area (see Table I).

TABLE I

Number of head reorientations as a function of distance from target. Twenty samples taken at random from easy (greater than 90% correct) and from difficult (less than 60% correct) problems.

<u>Greater Than 95% Correct</u>			<u>Less Than 60% Correct</u>		
		Total			Total
2-1 meters	1-0 meters	2-0 meters	2-1 meters	1-0 meters	2-0 meters
1	1	2	2	4	6
1	0	1	2	2	4
0	0	0	1	3	4
0	1	1	0	4	4
1	0	1	2	2	4
0	1	1	2	4	6
1	0	1	0	4	4
0	1	1	1	1	2
0	1	1	1	4	5
1	2	3	2	2	4
2	0	2	1	4	5
3	2	5	3	4	7
1	0	1	4	2	6
2	0	2	1	3	4
2	0	2	1	4	5
1	0	1	3	2	5
3	1	4	1	2	3
2	0	2	1	1	2
1	0	1	1	8	9
2	1	3	0	3	3
<u>$\bar{X}=1.20$</u>	<u>$\bar{X} =.55$</u>	<u>$\bar{X} =1.75$</u>	<u>$\bar{X} =1.45$</u>	<u>$\bar{X} =3.15$</u>	<u>$\bar{X} =4.60$</u>



TIME (sec.)
PULSE RATE

0
60

.5
60

1.0
60

1.5
60

2.0
65

2.5
60



TIME (sec.)
PULSE RATE

3.0
60

3.5
65

4.0
65

4.5
75

5.0
120

5.5
150



TIME (sec.)
PULSE RATE

6.0
150

6.5
150

6.75
400

7.0
100

7.5
30

8.0
30

Figure 5 Animal position and associated pulse rate at 0.5 second intervals during the last 2 meters of a run on a 0.32 cm brass target compared to the 0.22 cm thick copper standard target.

Past observations of echo ranging behavior in *Tursiops* have given the impression that the rate of emitted pulses increases as the range to the target decreases. Measurements of pulse repetition rate as a function of range from the target were made from the video-audio tapes collected during this study. In general these data agree with earlier observations. However, the mean pulse rate remained quite constant (60 per second) at ranges greater than 40 cm from the targets increasing to 400 per second and falling rapidly to 100 per second within the last 40 cm of the test runs.

Photographs taken at 0.5 second intervals during the last two meters of a 0.32 cm brass versus standard target are presented with the associated pulse rates in Fig. 5. Mean pulse rates were somewhat higher for difficult discrimination than for easy discriminations, but the rates varied by as much as a factor of 2 at any range for the target comparisons tested. The variation of pulse rate as a function of distance from the target is shown in fig. 6 for 0.32 cm brass vs standard and 0.64 aluminum vs standard comparisons. These data seem to be in general agreement, except for variation of rate, with those presented earlier by Norris (See Norris et al this volume).

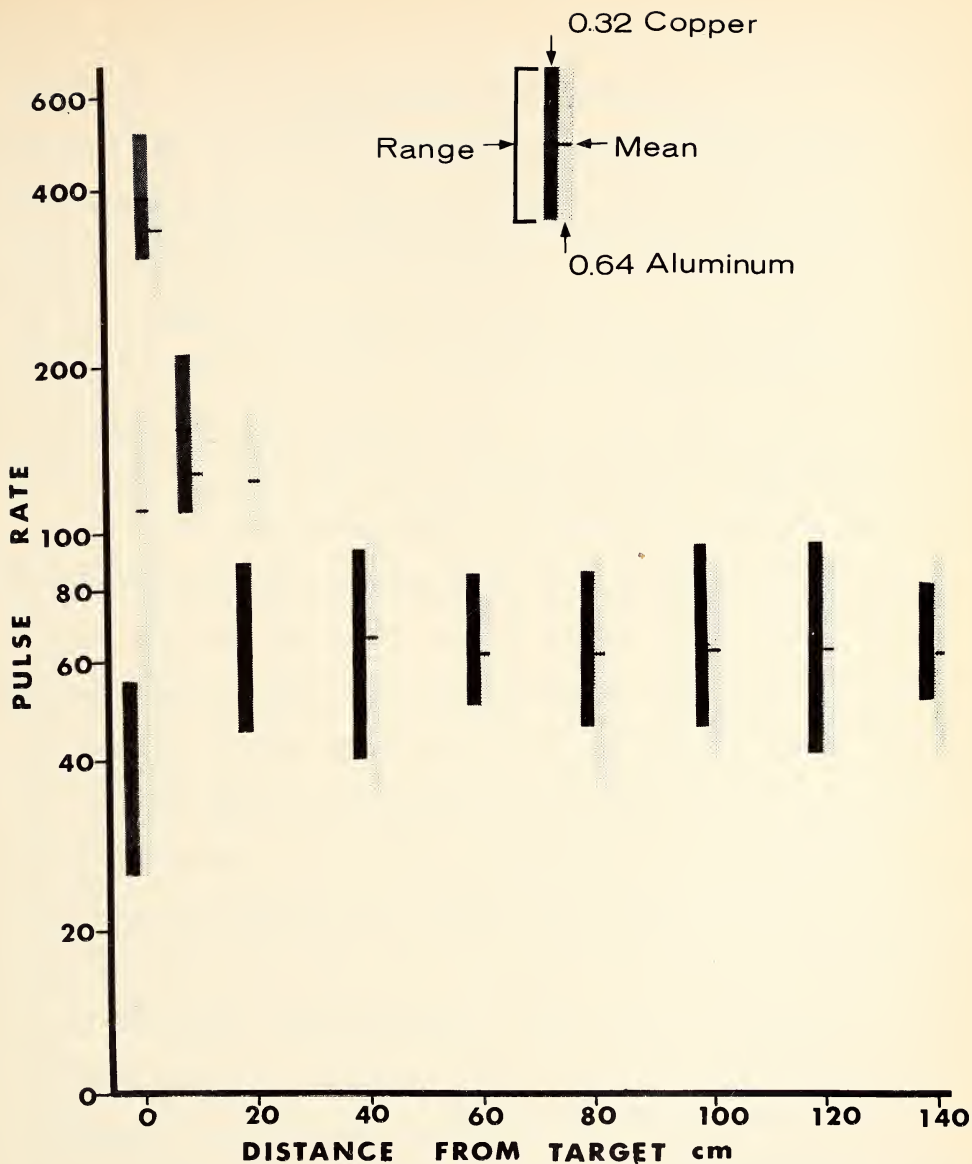


Figure 6

Mean and range of pulse rate as a function of distance from the target for 10 trials on 0.32 cm brass versus the standard and 0.64 cm aluminum versus the standard comparisons.

DISCUSSION AND CONCLUSIONS

Using operant conditioning techniques, it was possible to test with some consistency the ability of a blindfolded dolphin to select a standard target when paired with a wide assortment of comparison targets which varied theoretically only in the intensity of the echo. Within the limits of the targets available and the experimental design used, an absolute threshold of sonar discrimination based on differences in echo strength was approached but not adequately defined (Fig. 3). Determination of a true absolute threshold for this parameter of detection would require a series of comparison stimuli which varied in reflectivity from the standard in smaller increments than were used in this study.

When comparing aluminum targets to the standard 0.22 cm thick copper target the animal's performance was always greater than 90% correct even when the reflectivity of the comparison target (0.79 cm aluminum) was essentially identical to that of the standard. We must assume, then, that the animal was able to make the discrimination based on information other than reflectivity. When comparing copper targets to the standard, the performance dropped to chance at differences of reflectivity of 6%

and less. Although many explanations may exist to explain this apparent paradox, the utilization of phase information by the animal as suggested by MacKay (4) is one of the main possibilities we have considered. In order to achieve a reflectivity close to that of the standard copper target, the aluminum target had to be increased in thickness by a factor of almost four. With such a difference in thickness and its possible effect on the shape of the reflected pulse, enough information might be generated to account for the high levels of performance. (See Johnson, C. S. this volume).

In addition to the performance scores, the difficulty of the discrimination presented to the animal was denoted by very pronounced changes in the orientation and search behavior that accompanied the discrimination task. As the apparent difficulty of the discrimination increased, the scanning behavior of the animal became more pronounced. This included gross changes in the position of the whole body as well as the head. This was reflected in an increase in the mean time necessary for the animal to travel the last two meters to the target and make a selection (Table I).

There was a general increase in the emitted pulse rate as the animal approached the targets, and slightly

higher rates were achieved during difficult discriminations. However, the variability of pulse rate at any time or distance from the target made it impossible to arrive at any conclusions as to the role of this factor in either the discrimination of targets or determination of range.

It is difficult to conceive of any discrimination task in the natural environment of the delphinid that could not be more than adequately dealt with by the capability demonstrated by the animal used in this experiment. The ability of the delphinid, as represented by *Tursiops*, to discriminate rather small differences in size has been demonstrated by Norris et al (this volume). The results of this study just described indicate that differences in texture, which would determine the amount of signal absorbed and thus the strength of echo reflected, should be quite apparent to the animal. Thus, rather detailed information about the nature of his surrounding and potential food would be available to the echolocating delphinid.

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ABSTRACT

A blindfolded Atlantic bottlenose dolphin, *Tursiops truncatus*, was conditioned to select consistently a 30 cm diameter, 0.22 cm thick copper plate when presented paired with other plates. Knowing the acoustic impedance of the seawater and the thickness and acoustic impedance of the metallic plates, it was possible by computation to select a series of targets (plates) which differed in acoustic reflectivity by a known amount from the 0.22 cm copper standard target. In a comparison of a 0.27 cm thick copper plate with the standard target, the animal made the correct response 60% of the trials, or essentially at the chance level. In a comparison of the standard to a 0.32 cm copper plate, however, the responses were correct in 75% of the trials. Maximum performance scores of 100% were achieved at comparisons of 0.32 cm aluminum and 0.64 cm brass to the standard. These latter comparisons represented the greatest differences in reflectivity above and below that of the standard target.

DISCUSSION
by
C. SCOTT JOHNSON

It has been shown by Evans and Powell (in the preceeding paper) that their experimental animal could not reliably distinguish a brass plate from their copper standard plate but could tell an aluminum plate from the standard. Since all three of the plates in question had the same theoretical sonic reflectivity over a wide frequency range it is apparent that information other than relative echo intensity must be used in these discriminations. It has been suggested (MacKay, 1965) that the animal might make use of the phase information in the echoes to make such discriminations.

I would like to discuss briefly the possible importance of phase in complex sonic pulses and its roll in target discrimination. Consider the simple situation in Fig. 1. Here a sonic pulse consisting of two frequencies is incident on a plate with parallel sides, part of the energy is transmitted and part reflected. In general the reflectivity of the plate will be different for the two frequencies and so will the phase shifts. For parallel plates the reflectivity and phase shifts can be calculated fairly easily (Officer, 1958) and so they are potentially good targets to study for this reason. Hence the incident, transmitted, and reflected pulses may be quite different from one another. Figure 1 does not represent any real situation but merely

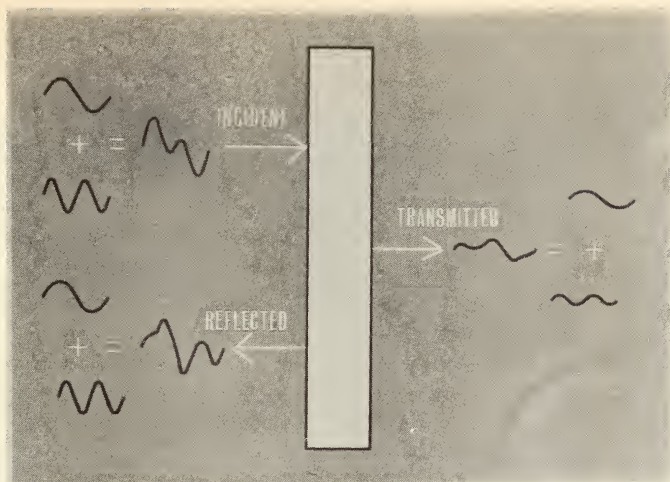


Fig. 2. - (a) Frequency spectrum of a "step" pulse. Here K and τ are constants and f is the frequency. (b) This shows the step pulse if all frequencies from 0 to ∞ are included. (c) If only the frequencies from 200Hz to 200kHz are used this pulse results.

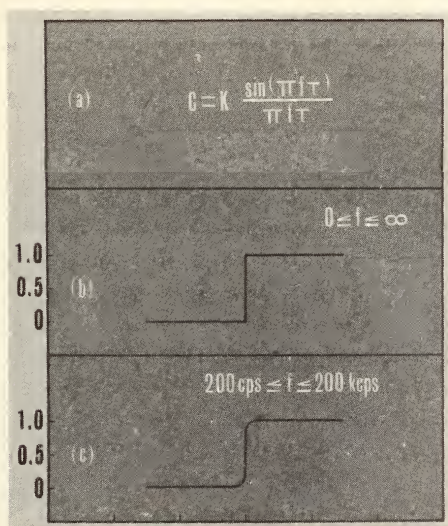


FIGURE CAPTIONS

Fig. 1. - This figure illustrates the changes in amplitude and phase of the reflected and transmitted components of a sonic pulse incident on a plate. The pulse consists of two frequencies. The two components of the incident, reflected and transmitted pulses are shown.

illustrates the principles involved in scattering sonic pulses from parallel plates. Since the pulses emitted by bats and porpoises may contain many frequencies let us consider a broad band pulse. Perhaps the simplest broad band pulse is a "step" function (Fig. 2b). This could be produced physically by connecting a battery to the terminals of a hydrophone. The active element of the hydrophone would be pulsed out (or in depending on polarity) and remain out until the battery was disconnected. This would produce a pressure wave in the medium (water or air) with a rapid on set and an exponential decrease to zero with time. The frequency spectrum is given approximately by the formula in Fig. 2a (Panther, 1965). Here r and k are constants and f is the frequency. This spectrum decreases as frequency increases. If all frequencies are present in the pulse one gets the step function in Fig. 2b. Using only frequencies from 200Hz to 200kHz one gets the somewhat rounded function in Fig. 2c.

If we scatter this pulse in water from a parallel section of air 1 cm thick we receive the results shown in Fig. 3. In Fig. 3a only the reflectivity of the section has been taken into account and in Fig. 3b only the phase shifts. In Fig. 3c both the reflectivity and phase shifts have been taken into account. It is obvious that if only the reflectivity of the scatterer is taken



Fig. 3. - This figure shows the results obtained from calculations which consider the reflection of the step pulse in fig. 1c on a 1 cm wall of air in water. (a) Shows the reflected pulse if only reflectivity is considered. (b) Shows the reflected pulse if only the phase shifts are considered. (c) Gives the resulting reflected pulse if both reflectivity and phase shifts are considered.



Fig. 4. - Here we have the calculated results from a step pulse incident on a 1 cm aluminum plate in water. In (a) only reflectivity is considered, in (b) only phase shifts and in (c) both reflectivity and phase shifts.

into account the incident and reflected pulses are very much alike but when the phase shifts are taken into account the reflected pulse is very much changed. Note that the pulse in Fig. 3c is inverted as well as distorted. This is because the scatterer has a lower acoustic impedance than the surrounding medium.

If we now scatter our step pulse from a 1 cm thick aluminum plate in water we get the pulses shown in Fig. 4. Here again in Fig. 4a only the reflectivity is considered, in Fig. 4b only the phase shifts and in Fig. 4c both reflectivity and phase shifts are considered. Here the pulse is not inverted because the acoustic impedance of aluminum is higher than water. However, much less of the acoustic energy is reflected from aluminum than air because the acoustic impedances of aluminum and water are much closer than air and water.

Let us now apply these simple theoretical considerations to the experiment performed by Evans and Powell. In this experiment parallel plates of aluminum, copper, and brass were used. The porpoise was unable to distinguish between a 0.32 cm brass plate and the standard 0.22 cm copper plate. It did however successfully distinguish the standard plate from a 0.79 cm aluminum plate. All three of these plates have the same reflectivity over a wide range of frequencies. Figure 5 gives the results

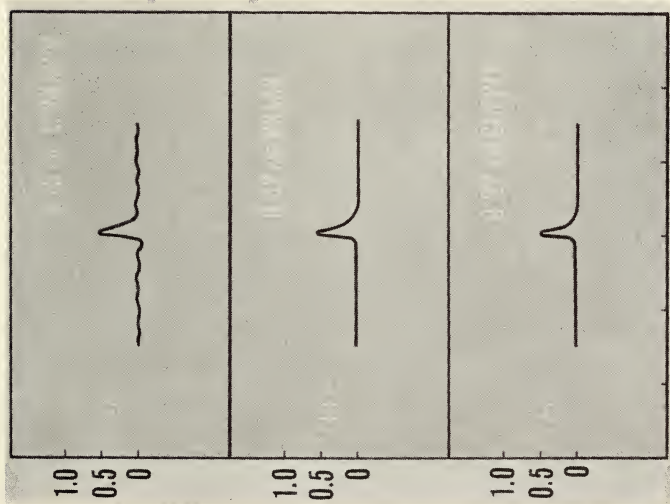


Fig. 5. - These are the calculated reflected pulses resulting from a step pulse incident on (a) a 0.79 cm aluminum plate, (b) a 0.32 cm brass plate, and (c) a 0.22 cm copper plate in water. Both reflectivity and phase shifts were taken into account. These pulses would be identical if only reflectivity were considered in the calculations.

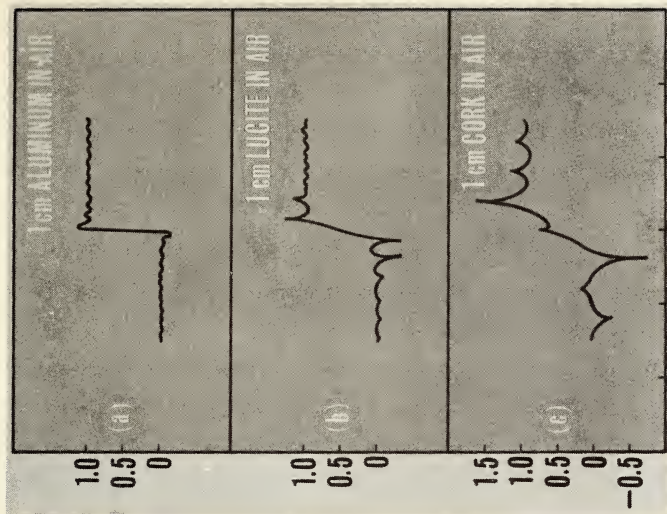


Fig. 6. - These are the calculated reflected pulses resulting from a step pulse incident on, (a) a 1 cm aluminum plate, (b) 1 cm lucite plate, and (c) a 1 cm cork plate in air. These pulses would be identical if only reflectivity were considered in the calculations.

obtained from theoretically scattering a step function pulse containing frequencies from 200Hz to 200kHz from the three plates. In each case shown both the reflectivity and the phase shifts have been taken into account. The pulses from brass and copper are very much alike while the pulse from aluminum is different in that it contains some definite ringing structure. While this isn't a very dramatic demonstration it does show a difference between aluminum, brass, and copper due to phase shifts. If only reflectivity were taken into account the pulses would of course be identical. It must be remembered at this point that the step function pulse was chosen for simplicity and not because it represented the actual pulses used by the porpoise in making the discrimination. If a pulse with more energy in the higher frequencies had been used the differences would have been larger. Calculations taking into account reflectivity and phase shifts using actual pulses emitted by the porpoise during the experiment are being made. Also it should be noted that we have considered only normal incidence. Taking into account the angular distribution of the various frequencies components in actual pulses may be important.

Figure 6 shows the results obtained from scattering the step function pulse from 1 cm aluminum, lucite, and cork plates in air. These results show a marked difference



Fig. 7. - This picture shows the porpoise, *Turstlops truncatus*, approaching an air filled rubber ring. The porpoise is shown wearing suction cup blindfolds. The circles are 20 cm apart. The TV camera and hydrophone are shown at the right of the picture.

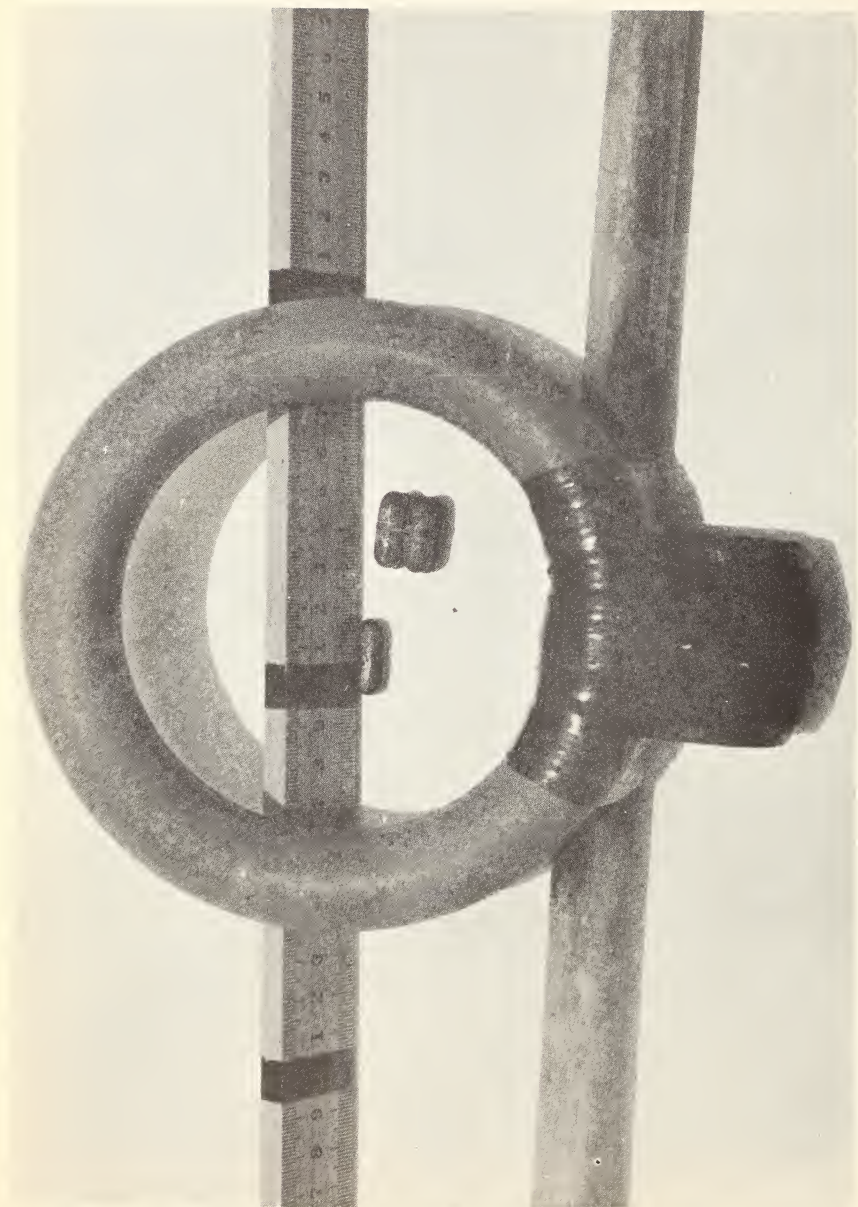


Fig. 8. - These are the three targets used. The meter stick indicates the sizes of the targets.

from one to another and indicate the possible importance of phase shifts to bats. Here again the pulse would be identical if only the reflectivity were taken into account.

Let us now consider the roll of pulse rate in porpoise echo ranging. This has been mentioned by Mr. Evans and Dr. Dziedzic. A simple experiment was conducted to try to determine the relation, if any, between pulse rate and target range. This experimental arrangement is shown in Fig. 7. A porpoise blindfolded with suction cups was trained to retrieve small objects. In Fig. 7 the porpoise is shown approaching a weighted air filled rubber ring. The concentric circles are 20 cm apart. The sound emitted by the porpoise and its position relative to the target were recorded simultaneously on video tape via the TV camera (lower right center) and the hydrophone (far right) (Fig. 7). This experiment was conducted with the assistance of Clark Bowers and W. E. Evans who helped a great deal with the data analysis also.

Three targets were used in the experiment and these are shown in Fig. 8. The largest was the weighted foam rubber ring with a 40 cm long stick attached. The smallest target was a single Squib vitamin pill and the third target was four vitamin pills tied together as shown in Fig. 8. A meter stick is shown in the figure to indicate the target sizes. The porpoise retrieved the ring by picking it up on his rostrum. The two smaller targets he

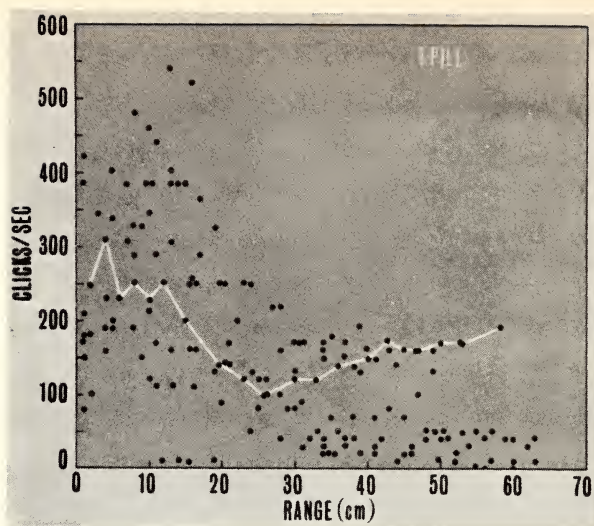


Fig. 9. - This figure gives the click rates in clicks per second versus range for the nine runs using the single pill. Straight lines have been drawn connecting the points for one of the nine runs.

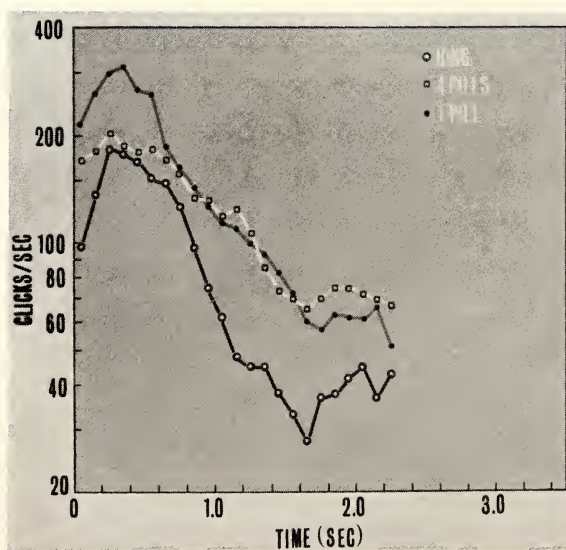


Fig. 10. - Semilog plot of click rate versus time before reaching the target for the ring (Open circles), four pills (crosses), and single pill (closed circles). These are averages of all the runs in each case.

picked up in his mouth. Nine data runs were taken with the single pill and six each with the four pills and the ring. Pulse rates versus time were determined from sonographs of the audio recordings and the animal's position versus time was determined from the video recordings. From these two sets of data the pulse rate versus distance and the speed of the porpoise could be determined at any time or position relative to the target. In Fig. 9 the click rate in clicks per sec has been plotted against range from the target in cm for all nine of the runs taken using the single pill. Straight lines have been drawn connecting the points for one of the nine runs. There is a great deal of scatter in the points plotted in Fig. 9 and a great deal of variability in the pulse rates for a given run. While the pulse rates do in general increase with decreasing range the great variability in rate from run to run and within the individual runs make it extremely doubtful that the animal makes use of pulse rate in its target range determinations. The great variability in pulse rate also would make one wonder if the time difference tones suggested by Nordmark (Nordmark, 1961) are used either. However, this possibility is not ruled out.

In fig. 10 the log of clicks per sec averaged for all the runs with each target is plotted versus time before the animal's rostrum becomes even with the target. At time

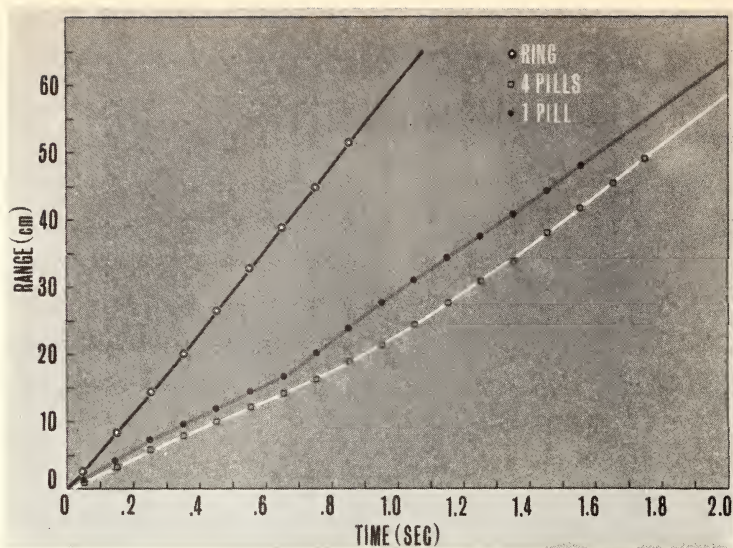


Fig. 11. - Plot of the average range versus time for all of the runs in each case. The animal's speed for the ring runs (open circles) was approximately 60 cm/sec while it was only about 30 cm/sec for the four pills (crosses) and single pill (closed circles). Note the decrease in speed at about 30 cm.

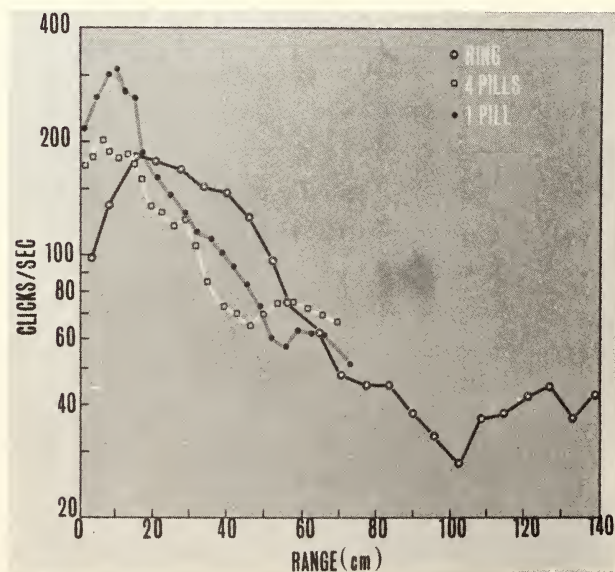


Fig. 12. - Plot of click rate versus range averaged for all the runs taken with the ring (opened circles), the four pills (crosses), and the single pill (closed circles).

zero the animal's rostrum is even with the target (zero range). Two things should be noted from Fig. 10. First the pulse rate becomes maximum in each case about .1 to .2 sec from the target and decreases as the target is approached. The second thing to note is that the click rate starts to increase in each case at almost the same time, 1.6 sec from the target.

Figure 11 gives a plot of range from the target versus time averaged in each case for all the runs for each target. From this plot the porpoise's speed can be estimated. The average speed for the single pill and four pill runs was about 30 cm/sec and for the ring 60 cm/sec. The plot of log average click rate versus range shown in Fig. 12 was obtained from the data in Figs. 10 and 11. Here the velocity was assumed to be constant and extrapolated to ranges greater than 60 cm. Here we see that the click rates at a given range may vary by as much as a factor of two for the three targets. If click rate and range were related one would not expect this variation.

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ABSTRACT

The possible use of phase information by the porpoise in discriminating between metallic plates has been investigated on the basis of simple theoretical considerations. While the results indicate that there are definite differences in reflected pulse shapes due only to phase differences more detailed calculations than the present ones should be made. Measurements of echolocating pulse rate versus range and time before target contact have been made. While the pulse rates do in general increase with decreasing range it is unlikely that the animal makes use of pulse rate for range determination. The time before target contact seems to be the dominant factor rather than range in its effect on pulse rate. This experiment does not indicate how the animal determines range.

III

Les caractéristiques générales
des signaux acoustiques d'orientation
et les performances
des sonars dans le règne animal

General features of orientation sounds
and the performance achieved
by the animal's sonar

GENERAL CHARACTERS OF ACOUSTIC ORIENTATION SIGNALS AND PERFORMANCE OF SONAR IN THE ORDER OF CHIROPTERA

by
F. P. MÖHRES

Sonar systems do not exist in all members of the order of Chiroptera. According to our present knowledge all members of the suborder of bats, Microchiroptera, possess more or less efficient sonar systems. Up to the present time, the use of sound for object discrimination has been found only in the Genus Rousettus of the suborder of fruit-bats, Megachiroptera. These fruit-bats use sonar as a complement to their well developed dim-light vision. All other fruit bats rely totally on vision.

Characters of orientation signals in bats show a rather wide variety, which up to the present has only been studied in a general way. Of the 16 families of Microchiroptera only four, Vespertilionidae, Rhinolophidae, Megadermatidae and Phyllostomatidae, have been rather thoroughly examined. More sporadic data exist for the other families.

For convenience we will discuss families for which we have rather complete information.

1. Vespertilionidae (very similar to Noctilionidae and Molossidae)

Orientation sounds of the Vespertilionidae are generally rather short (1-3 msec.). The signals get longer when the bats fly in open space far from obstacles. On the average they are longer in species which fly at high velocity, and hunt on routes allowing free and unimpeded flight (Nyctalus noctula). The signals usually have a rather complex structure. They consist of a more or less extended band of different frequencies, mostly in the range of 35 to 80 kHz. Amplitude rises very steeply in the beginning, declining less steeply at the end. The sounds show a very definite frequency-modulation. Frequency is high at the beginning, going as high as 80 kHz. It decreases more or less gradually to half the value towards the end. Thus, the frequency decline within the signal is about one octave.

Intensity of signals generally is rather high. The sound pressure at a distance of 5 cm from the mouth of a Myotis lucifugus has been found to be as high as 110 dB. A few species (Plecotus, etc.) have rather weak signals consistent with their special hunting patterns.

Repetition rate of orientation signals varies with the situation. Before flight a bat searching around may produce not more than 10 signals per second. The repetition rate during flight may vary between 10 and 50. Approaching a goal or obstacle, the bat may increase the repetition rate up to 200 or 300/sec. To give general values for the whole family is scarcely possible, as differences between the species are rather great. However, we can say, that in this group an increase of the information flux obviously requires an increase of repetition rate, i.e. more signals per time unit.

In general, vespertilionid bats emit acoustic signals through the mouth. Only a few species are able to alternatively use the nasal pathway. As far as can be told by examination, the sound-producing apparatus in all Microchiroptera, is the larynx.

To generally characterize the efficiency of the sonar system in vespertilionid bats is rather difficult, as information is restricted to a few species. Exact values have been given for Myotis lucifugus. These bats seem to be unable to perceive wires of less than 0,12 mm diameter. This value lays within the range which has been found in tests with other species of Vespertilionidae.

2. Rhinolophidae

Studies of the ultrasonic orientation mechanism in Rhinolophidae or horseshoe-bats have first of all revealed remarkable differences in the signals and locating mechanisms of the two groups of microchiroptera, and have initiated comparative studies in this field.

Horseshoe-bats never emit their orientation signals through the mouth, but through the nostrils. The signals are characterized by their long duration, the presence of only one intense frequency, and the nearly complete absence of frequency-modulation and amplitude modulation. The level of the constant frequency varies from species to species, and only to a small degree within the species from individual to individual. In the bigger European Horseshoe-bat (Rhinolophus ferrum equinum) the frequency is about 84 kHz. The smaller Rhinolophus hipposideros emits pulses on the average of 108 kHz. The very tall Rhinolophus hildebrandt from Kenya has a frequency of 38 kHz. Harmonics are nearly totally suppressed. Thus orientation signals have the character of very pure tones, in which only the first and the last waves show frequency-modulation. A final outburst, resembling somehow an orientation signal of vespertilionid character, may be present when orientation sounds of horseshoe-bats are produced with high intensity.

Intensity of signals varies with the size of the species. Compared with vespertilionid bats of the same size, the intensity is very high. In Rhinolophus ferrum equinum the sound pressure at a distance of 5 cm in front of the nostrils is about 115 dB. Rhinolophid bats are fitted with a kind of focusing apparatus, which is represented by the "horseshoe", a reflector-like structure surrounding the nostrils built up by connective tissue and muscle-fibres. This focusing apparatus allows the emitted sound to be concentrated into a very narrow bundle, or even to a far reaching beam. Thus, horseshoe bats can locate over a distance of several meters. In Rhinolophus ferrum equinum it is evident that the bat can recognize objects to a distance of about ten meters.

The duration of signals is long as compared with all other groups of bats. In the non-flying bat the orientation sounds last as long

as 50 - 60 msec on the average (Rhinolophus ferrum equinum). Signals can have a maximum length of 100 msec. During flight signals usually are shorter, and in the approach phase they can be reduced to 10 msec. Intervals between the signals are rather short compared with the duration of signals. Thus, signals of rhinolophid bats show a tendency to continuous tones.

The efficiency of the sonar system seems to be more perfect than in vespertilionid bats. That horseshoe-bats can identify objects by their sonar over a distance of several meters has already been mentioned. Rhinolophus ferrum equinum can detect wires of no more than 0,06 mm diameter and it fails to detect wires of 0,05 mm. The family Hipposideridae resembles the Rhinolophidae in many ways: They possess similar noseleaves and movable ears, but orientation sounds are more complicated, as they consist of two distinguishable parts: an initial part, which is a pure tone of very high frequency, and a terminal part resembling the orientation signals of Vespertilionidae. A detailed investigation of the sonar of Hipposideridae is in preparation in our institute.

3. Megadermatidae

Megadermatidae or False Vampire Bats belong to the same superfamily as the Rhinolophidae. They emit their sonar signals only through the nostrils, and they, too, possess a megaphone-like structure of the nose-leaf acting as a beaming device.

The Megadermatidae use signals of very short duration. Megaderma lyra, when resting, emits orientation sounds which average 0,67 msec. During the flight the signals are somewhat longer (average 1,18 msec). In the approach-phase pulses are continuously shortened.

Frequency structure of the signals shows special features. The signals consist of 3 or 4 harmonic frequencies. In the species mentioned, the basic frequency is about 20 kHz, the other harmonic

laying at 40,60 and 80 kHz. The highest frequency present is the most intense one. Frequency-modulation is nearly absent. The envelope form of the signal, i.e. the course of amplitude, may be ovoid or resemble more the shape of vespertilionid signals.

Repetition rate changes from 10 per sec in resting position to 10 - 80 during flight, the highest values belonging to the approach phase.

In spite of the low intensity of signals, the efficiency of the sonar system is rather good. Megadermatid bats can detect wires of 0,06 mm diameter, but the sonar does not operate over long distances. The limit for object discrimination seems to lay in a distance of about two meters maximum. As these bats fly rather slow and prefer hovering, there may be no real necessity for orientation over a longer distance.

4. Phyllostomatidae

Orientation signals of the Phyllostomatidae or American vampire bats show some resemblance to those of the Megadermatidae. The differences in this group are rather remarkable. The bat Phyllostoma hastatum, may serve as example of the first type. This bat is omnivorous, and the nose leaf shows some similarity with that of the Megadermatidae. Signal duration is in the range of vespertilionid bats (1-3 msec), but the signals lack frequency-modulation which is so characteristic of the Vespertilionidae. Harmonics are present, basic frequency being in the range of 10 - 15 kHz. The harmonic content seems to vary. Some pulses contain only the basic frequency plus second and third harmonics, others are restricted to the higher harmonics up to 90 -100 kHz. In general, the shorter the sounds, the higher is the harmonic range. The repetition rate shows no peculiar features. Intensity is medium, and sound pressure measured at a distance of 50 cm is 1 dyn/cm^2 .

Group	Duration of signals	Intensity	Frequency structure	Emission
Emballonuroidae	short-medium	high	slight frequency-modulation or none, harmonics present	mouth
Phyllostomatoidea	medium-short	medium-little	FM, slight or none	nose
Rhinolophoidea	short, medium, long	high-medium	no FM, few harmonics	nose
Vespertilionoidea	medium-short	high	frequency-decline very definite	mouth, rarely nose

The subfamilies, Carolliinae, Stenoderminae, Glossophaginae, and the related family, Desmodontidae, are remarkable for their extremely weak orientation sounds. These sounds show close similarity in frequency structure. Signals contain several clearly visible harmonics which show variation of presence and sometimes change even within one single pulse. The highest recorded frequencies are in the range of 100 - 120 kHz.

Wires of 0,175 mm could be detected. Whether this is the limit or not is not known.

5. Review of the sound characters in other groups

For other groups of Chiroptera the data are still rather sporadic. It may be useful to condense our present knowledge into the form of a table, referring to the superfamilies.

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ECHOLOCATION IN AN ATLANTIC BOTTLENOSE PORPOISE DURING DISCRIMINATION

by

Kenneth S. NORRIS, William E. EVANS
and Ronald N. TURNER

Introduction

Knowledge of cetacean echolocation capability has rested primarily upon gross behavioral observations correlated with the presence of sound emission (for example, see Schevill and Lawrence, 1956; Kellogg, 1961; and Norris et al., 1961). Analysis of sounds implicated in echolocation has generally been casual and almost nothing is known of sequential changes that occur when a porpoise closes upon a target. Controlled experiments upon the details of click trains are wholly wanting, though some details of arbitrarily selected sounds exist (Kellogg, Kohler and Morris, 1953).

Recently, two of us completed an experiment in which an Atlantic bottle-nose porpoise was required to accept blindfolds and perform a discrimination between nickel steel ball bearings of two sizes suspended beneath the water surface (Turner and Norris, 1966). Eventually this animal was able to give error-free performance at a disparity of 5.40 cm vs 6.35 cm diameter ($2 \frac{1}{8}$ vs $2 \frac{1}{2}$ "), with performance falling off to 77% success at a disparity of 5.71 cm vs 6.35 cm ($2 \frac{1}{4}$ vs $2 \frac{1}{2}$ "). During this test a series of sound recordings was made which allow analysis of some details of echolocation.

As the subject swam in toward a pair of levers extending 15 cm into the water behind and between which the stimulus spheres were suspended 25 cm below the surface, recordings were taken of the entire sequence of sound emission (Fig. 1). The subject was required to press the lever on the side of the largest sphere. Several replicate recordings were made for runs at

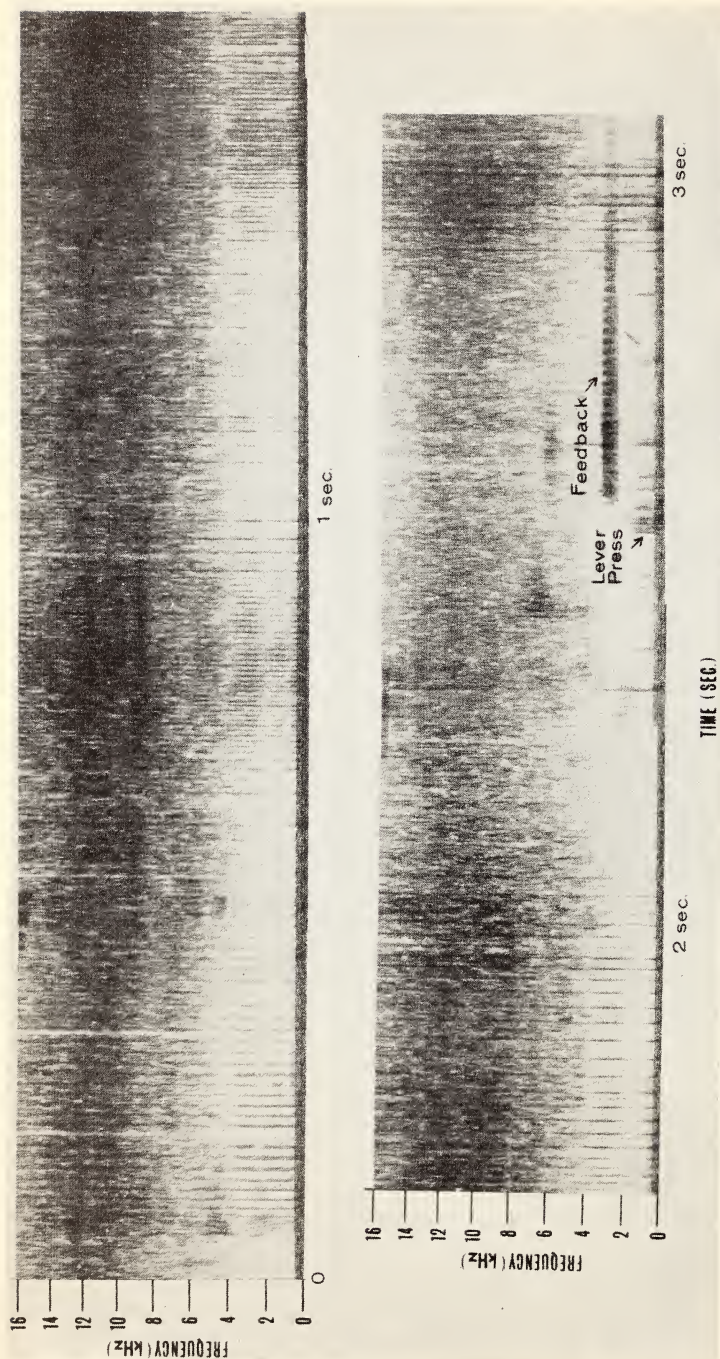


Fig. 1 Sequence of sound emission during a discrimination run. Note periodic increases in repetition rate and blank period just above 2 second marker. This is followed by the sound of the lever press and the trainer's whistle (feedback), and then a series of orientation clicks above the 3 second marker. Sphere disparity, 2 vs. $2\frac{1}{2}$, correct response.

each stimulus disparity level, thus allowing statistical treatment of observed variation in the associated click trains. Comparison between run series at different disparity levels allows appraisal of features of click trains that apparently are related to the difficulty of discrimination.

Our data are not as complete as we wish them to be. Underwater sound gear that could record the entire frequency range of the emitted signals was not available to us. Likewise unavailable was photographic monitoring equipment allowing precise localization of the animal's position at all times. Recordings during two of the stimulus pair states proved unusable because of instrumental difficulties (5.71 cm vs 6.35 cm and 6.35 cm vs 6.35 cm). Even so, a reasonably complete picture was obtained of many of the signal characteristics used by the porpoise as it swam toward the stimulus pair. The free-standing circular plastic tank was a highly reverberant environment, as is evident from the taped records. Both complexly reflecting sounds from within the tank and outside sounds transmitted through the tank walls were present. In spite of this complex sound environment the porpoise was able to discriminate at an impressive level.

Before presenting and analyzing the data our usage of some special terms needs to be defined.

Click train. Each entire unbroken series of clicks emitted during the course of a discrimination. In this experiment nearly every discrimination run was composed of a single click train.

Burst. Within each click train more-or-less distinct subdivisions can be discerned in which repetition rate cycled from low to high levels and back again.

Click. A short plosive sound often composed of two parts in Tursiops, typified by almost instantaneous rise time.

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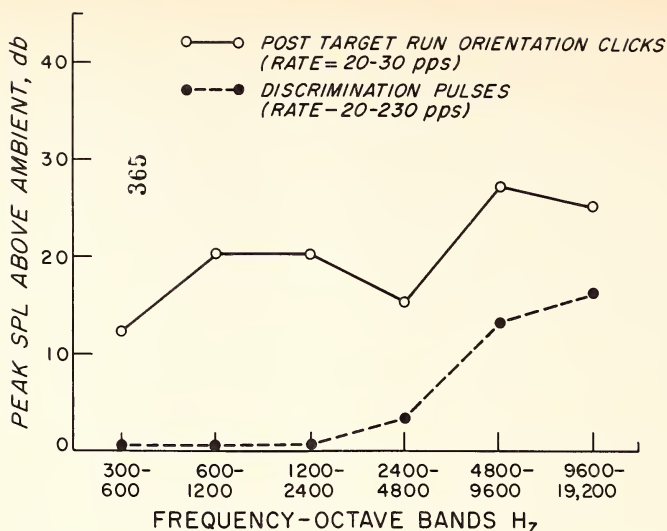


Fig. 2 Octave band analysis of the low frequency portions of orientation and discrimination clicks.

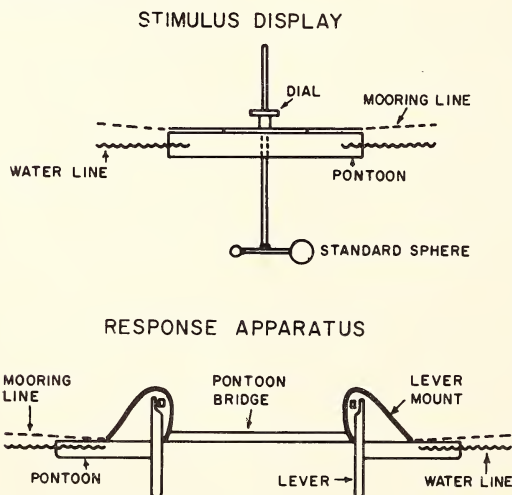


Fig. 3 Spatial relations of level array and test spheres.

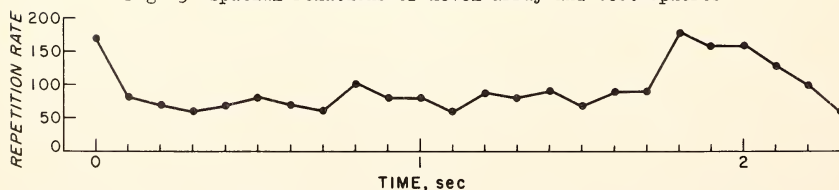


Fig. 4 Changes in repetition rate during a successful 2.3 sec discrimination run at sphere disparity of 2.0" vs. 2.5". Note the initial high rate rapidly subsiding to a relatively uniform level and then the final rapid burst just before press of the left lever.

Interclick interval. The time period between the end of one single or double click and the onset of another.

Intraclick interval. When a double click is emitted that lasts, altogether, a millisecond or two, the intraclick interval is taken as the time period between the end of the first major spike and the beginning of the last in the pair.

Discrimination click. A tentative term for clicks produced by the animal during discrimination.

Orientation click. A tentative term for clicks produced when the subject apparently is orienting to general features of the environment. Characteristically, in the human audible region, these clicks are of high amplitude and long duration, and low frequencies are emphasized as compared to discrimination clicks (Fig. 2).

Circuit time. The time required for the onset of a click to travel from the emitting source to a target and back to the animal's ears.

Materials and Methods

The porpoise used in this experiment, an adult female Atlantic bottle-nose porpoise (Tursiops truncatus Montagu) weighed approximately 300 lbs, and was 7 ft. total length. She was housed in 7.3 m diameter x 1.2 m deep plastic swimming pool on the University of California, Los Angeles campus. Tank water was compounded of tap water and water-softener salt, replenished completely every two to three weeks and held at about a salinity of 35 o/ooo. Water temperature varied somewhat around the figure of 20° C.

The subject was blindfolded with cast RTV silicone rubber suction cups pressed lightly over her eyes. The animal was then required to circle the tank counterclockwise and home in on the stimulus display, which consisted of an inverted T-shaped rod at each end of which was mounted a nickel-steel ball

bearing. One ball bearing (the reference sphere) was always 6.35 cm in diameter, while the other bearing varied in size according to the test situation. Sizes used varied from 3.18-5.71 cm diameter. The side on which the reference sphere appeared was varied according to a limited random series. The bearings were 12.7 cm apart, measuring from the inner curve of each. Sixty cm in front of the stimulus display was located a pair of cylindrical lucite levers, mounted on floats 60 cm apart (Fig. 3). The subject was required to press the lever on the side where the reference sphere appeared. Her collateral behavior became quite stereotyped during the tests. She circled the tank, about 1.8-2 m from the edge, rose to the surface for a single respiration at about 2.4-3 m from the stimulus display, then swam toward the spheres underwater. When the tip of her snout was an estimated 45-60 cm from the levers she either changed course abruptly and pressed the most distant lever with her rostrum or continued directly ahead and pressed the nearest lever. Occasionally she refused to make the required discrimination. After an error, the reference sphere was always presented again on the same side though the data indicate that the animal did not learn this (Turner and Norris, 1966).

It was often possible to predict when the porpoise would make an error by watching for variations in her collateral behavior. Such error-related behavior usually consisted of her varying the position of the respiration so that a shorter-than-usual distance was available for the click train emission. Click trains were shorter in this situation. Other errors were made when she swam closer to the tank wall than usual and thus approached the display at a greater than usual angle. Once the correct lever was pressed, a whistle reinforcement was immediately given by the operator. This can sometimes be heard on the taped record. The porpoise then withdrew her rostrum from the

lever and continued the counterclockwise circle. At this time a single surf smelt (Hypomesus pretiosus) was thrown in the tank. As the animal left the lever she gave a very characteristic burst of loud, long-duration orientation clicks, much different in frequency and duration than the clicks used during discrimination runs.

Once the reward fish hit the water the animal localized upon the splash while emitting a discrimination click train, sometimes much more prolonged and with bursts of higher repetition rate than those used during sphere discrimination. The click train was especially prolonged and of fast repetition rate if the fish floated and had to be discriminated from the surface ripples.

If the porpoise made an error, the stimulus display was immediately removed from the water and a "time-out period" instituted as punishment.

During selected runs, which included both correct responses and errors, recordings were made of click trains and the following orientation clicks, using an Atlantic Research Corp. pressure transducer, model LC-10, coupled to a Uher 4000S portable tape recorder, through a battery powered preamplifier, Ballantine Model 220B. The response of this system is limited by the recorder to a ± 2.5 db from 50 Hz to 20kHz at 7.5 ips (19.05 cm/sec). Since the frequency and transient response limits of the system are well below those demonstrated for some porpoises (Norris and Evans, 1966) the signals recorded in this study do not give a complete representation of the signal available to the animal for discrimination.

Data analysis was performed with a Minneapolis-Honeywell "Visicorder" recording oscillograph mod. 1508. The visicorder was equipped with a M 8000 galvanometer with a flat response from DC to 5000 Hz. Setting tape playback at 1/4 or 1/8 recording speed raises oscillograph response to 20 to 40kHz while

the time axis is stretched 4 to 8 times real-time values. This expanded time scale greatly facilitates the study of individual clicks, the accurate measure of click duration, repetition rate and rise time. In this recorder photosensitive paper is fed at a controlled speed past a moving spot of light reflected from a mirror galvanometer. Long click trains were analyzed using paper speeds of 25 to 2000 mm/sec at 1/8 recording tape speed. This yielded a real time paper speed of 200 mm/msec to 16,000 mm/msec. In some cases tapes to be analyzed had high ambient noise. Variable filters (Kron-Hite mod. 315A) were introduced between the tape playback and the oscillograph. With suitable frequency setting much of this noise could be eliminated with minimal degradation of the wanted signal. Octave band analysis was made using the same filters.

It should be noted that as the upper frequency response of the oscillograph is effectively increased by slowing of the data tape, the low frequency limit of the tape is increased by the same factor, e.g. at a speed reduction of 8x frequencies below 400 Hz are lost. Also in many cases click durations are contaminated by the reverberant nature of the test environment because it was difficult to resolve that part of the click signature that was directly of animal origin and that due to reverberation.

Results

Successful discrimination runs were made by the porpoise which involved from 1.1 to 4.7 second click trains given at repetition rates that varied from 20/sec to 230/sec. Often, though not always, these click trains started at rates between 80-100/sec and quickly descended to 50-70/sec. Usually subsequent fluctuations in rate during the majority of the click train fell within 20/sec on either side of this lower level. Toward the end of many runs the rate rose rapidly to its peak at 130-180/sec and then dropped rapidly,

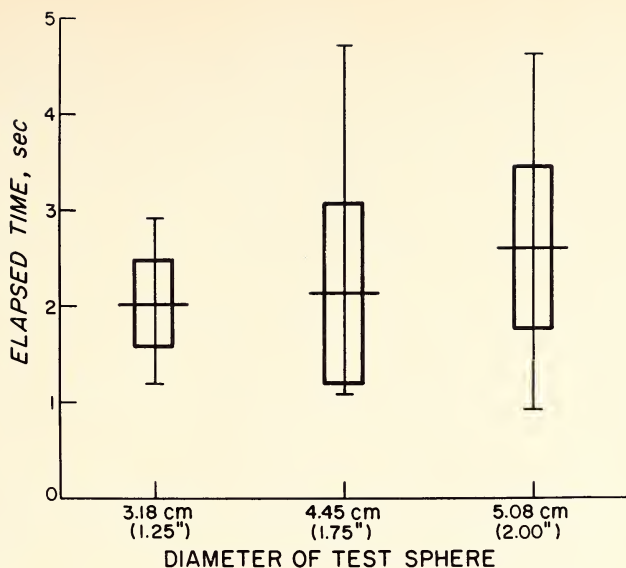


Fig. 5 Range, mean and standard deviation of successful discrimination runs at various sphere disparities.

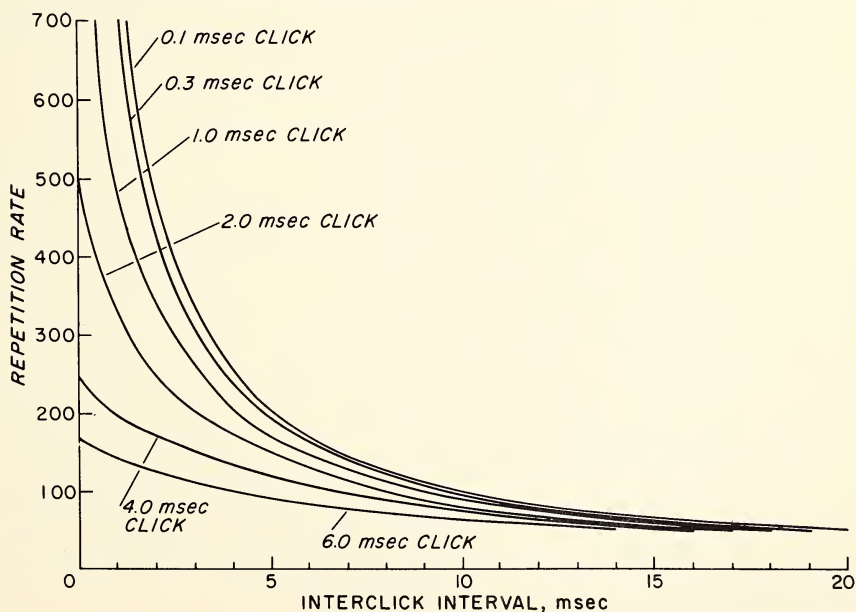


Fig. 6 Relations between repetition rate and interclick interval for clicks of various durations. Sea water, 20° C, salinity 35 o/ooo.

often to levels below 50/sec (Fig. 4). The animal was apparently silent for approximately the last 0.5-1 meter before the appropriate lever was pressed. As the animal turned away from the levers the slow orientation click train was emitted, followed by the click train of discrimination clicks directed at the fish reward.

Nine features of these runs have been considered. Some vary regularly in relation to stimulus disparity and may be manipulated by the porpoise during discrimination behavior in natural situations. The features considered are duration of click train, animal speed, repetition rate, click duration, interclick interval, intraclick interval, frequency, intensity composition of emitted clicks, and echoes.

Duration of click train. The regular respiration made before a discrimination run is audible on most tapes and can be recognized on visicorder traces. Its cessation is taken here as the beginning of a discrimination run, since echolocation clicks began immediately after its completion.

For the simplest discrimination analyzed here (3.18 vs 6.35 cm) click trains were very uniform and of short duration, averaging 2.0 seconds, and ranged between 1.2 and 2.9 seconds (Fig. 5). The most striking feature of the more difficult runs (4.45 vs 6.35 cm and 5.18 vs 6.35 cm) was a marked increase in variability of click train length. While some trains at 5.18 vs 6.35 cm were short, these were mostly errors. Three out of four click trains 1.4 seconds duration or shorter resulted in errors. Trains resulting in errors averaged 1.8 seconds duration while click trains of correct runs averaged 2.5 seconds. Long click trains were common, the longest being 4.7 seconds duration.

Animal speed. Approximations of locomotion speeds during discrimination runs can be made. The initial respiration was estimated by eye to be accomplished

between 8 and 10 feet from the lever apparatus. Since the animal did not seem to move this point of respiration farther from the levers on difficult problems, it must have slowed its locomotion somewhat. This was confirmed by observation as were the general range of calculated speeds. Average calculated speeds can be determined from elapsed time and the estimated distances as 3.1 miles per hour (111 cm/sec) for a stimulus pair disparity of 3.18 vs 6.35 cm and 2.5 mph (86.3 cm/sec) for 5.18 vs 6.35 cm. The slowest run took 4.7 sec, which converts to a speed of 57.8 cm/sec or 1.3 mph.

Repetition rate. Click repetition rates during discrimination runs averaged 65 clicks/sec for 3.18 vs 6.35 cm, 74 clicks/sec for 4.45 vs 6.35 cm, and 78 clicks/sec for 5.18 vs 6.35 cm. Even if the extreme rate of 230 clicks/sec is considered these rates are very low compared with published figures (Norris et al., 1961, 416 clicks/sec; Lilly, 1962, 1200 clicks/sec; Evans and Prescott, 1962, 525 clicks/sec). This difference seems to be related to the distance between the porpoise and the discriminated object. In these tests repetition rates reached much higher levels when the animal was searching for a fish than during discrimination of spheres. In the discrimination tests the animal never approached the target spheres closer than 60 cm, and it seems probable that the final high repetition rate burst often given was related to localizing the levers and not the spheres, though this cannot be said with certainty. When localizing the reward fish the porpoise continued to echolocate until shortly before grasping the fish, and often had to search diligently under the irregularities of the surface for floating fish.

During the majority of most discrimination runs repetition rates fluctuated within rather narrow values, punctuated here and there by bursts which

reached repetition rates 2-3 times this level. These base levels varied as sphere disparities varied. On the easiest test (3.18 vs 6.35 cm) the general rate between bursts hovered between about 30/sec and 70/sec. With lesser sphere disparity this base rate seldom dipped below 50/sec, and was generally found between 50/sec and about 80/sec.

No regular sequential change in repetition rate over the entire click train occurred as the animal closed upon its target, except for the commonly-observed burst of relatively high repetition rate clicks that closed the run.

Reasons for sequential changes in repetition rate might be the placement of the echo either in the interclick interval or the superposition of the echo upon the next following (Fig. 6) click. During a run from respiration to lever press the circuit time for a click hitting the spheres varied from 4.8 msec to 1.6 msec (Fig. 7). If we assume that the click was 1 msec in duration every click emitted by the porpoise would have the onset of its echo fall in the interclick interval until the very close range of 41 cm was reached, at which distance the returned echo would just arrive at the end of the outgoing click. This distance corresponds approximately to the estimated distance at which the animal broke for one lever or another and ceased to echolocate.

At a repetition rate of 60/sec, such a 1 msec click takes up only about $1/16$ of the time from its beginning to the initiation of the next click, hence repetition rates need not be especially precise while still maintaining the echo in the interclick interval, though the echo is certainly of longer duration than the emitted signal. In fact under these circumstances the click and the onset of the echo can overlap only at the very close range mentioned and more than 24 m away, where the echo would return during emission of the successive click. At the distance of 3.65 m from the spheres circuit

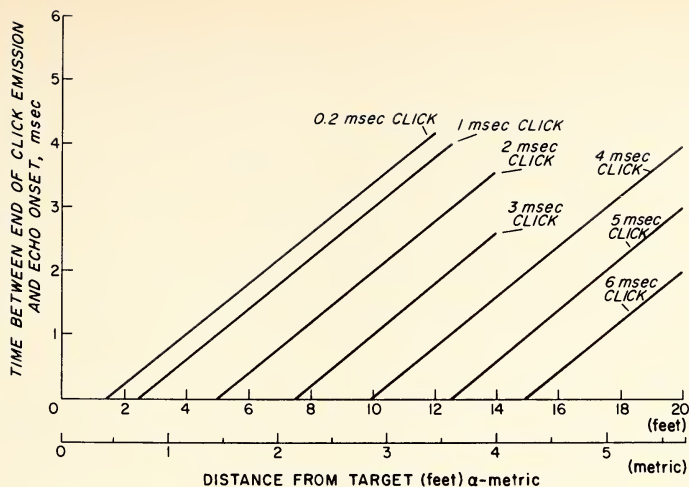


Fig. 7 Circuit time relations for clicks of various durations. Sea water, 20°C , salinity 35 o/ooo.

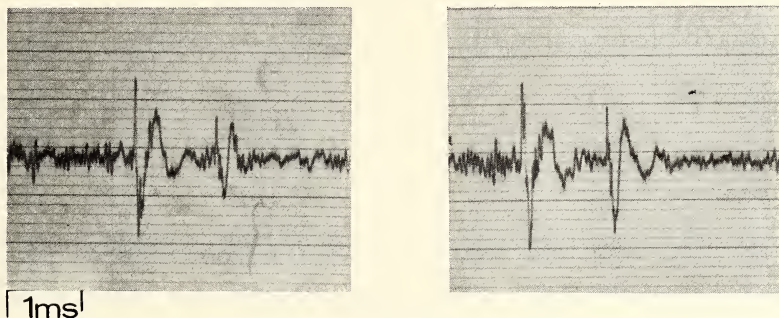


Fig. 8 Paired clicks recorded at sea off Santa Catalina Island, California, from Tursiops gilli. Repetition rate of click train; 40-50/sec.

1. RIGID BODY ECHO
2. SECONDARY ECHO RESULTING FROM VIBRATION IN SPHERE

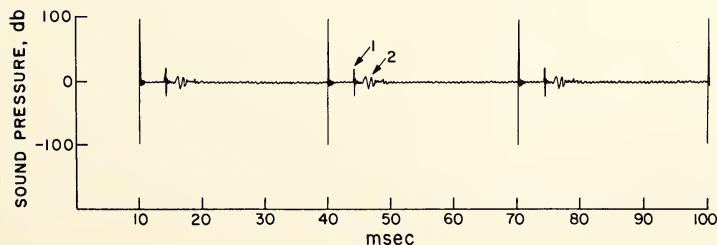


Fig. 9 Schematic diagram of a click train, showing click, rigid body echo, sphere signature and 4 msec space between click and echo onset, convertible to difference tone of 250 Hz. Target at 10' (3.3 meters), for sound at 5000 fps (1524 mps), repetition rate, 33/sec.

time is 4.8 msec and a repetition rate of 187/sec would be required to cause overlap, a situation never observed. The highest reading for repetition rates at initiation of click trains was 170/sec. However, analysis of echoes from ensonified metal spheres in water has been performed by Hickling (1964), and Hickling and Diercks (1966) and the major returning echo is about 5x the duration of the emitted signal, with perhaps significant energy still being returned after a duration of 8x the emitted signal. Thus, the rather long interclick interval found here will not always serve to contain the echo wholly at the initiation of a run but will contain the echo during most of the remainder of the run. Toward the end of each run, before the final high repetition burst occurs, the echo will cease at about the midpoint of the interclick interval or a little afterward.

The orientation click trains emitted as the porpoise turned away from the levers were composed of 8-15 clicks emitted at the very slow repetition rate, perhaps indicating their use for detection of relative distant objects or to contain long reverberant echoes in the interclick interval. Repetition rates during localization of reward fish were higher than those exhibited during discrimination runs and often exceeded 400/sec. These runs were often very long, usually because the animal had difficulty in locating the fish when it floated among the surface waves.

Click duration and structure. The highly reverberent environment of the tests makes it difficult to determine the total duration of clicks with precision. The clicks are clearly paired emissions whose peaks can be clearly seen above the background noise level. The same kind of paired signal has been recorded repeatedly from Tursiops recorded at sea (Fig. 8). At sea reverberation is often insignificant and more detail can be noted. It can be seen in such recorded signals that the click is often composed of two transient-like energy peaks each about 0.2 msec in length, with a

somewhat variable intraclick interval between. Further, it can be noted that the peak amplitude of the individual clicks is seldom equal. One might assume that this two-parted click represents different arrival time for two sound paths, say a direct path from the animal and one reflected from the nearby water surface. This does not seem correct as all cetacean species do not always produce double clicks in similar physical circumstances. For instance the rough-tooth porpoise (Steno bredanensis) usually produces single clicks (Norris and Evans, In press). Further, such single and double clicks have been recorded at different times in the same tank and recording situation depending upon which species was resident. Further, there seems to be no sequential variation in intraclick interval such as one would expect during the undulatory swimming of a porpoise closing on a target if travel paths are involved. Thus, we feel fairly confident that the double click is an actual emission feature of Tursiops and may relate to the shape or vibratory characteristics of the radiating structure, or to the frequency structure of the emitted signal.

Intraclick interval. As in the case of click duration, intraclick interval is difficult to determine with precision. In spite of the high background noise of our experiment it is possible to make estimates by measuring the time between the prominent spikes of a double click. Such measurements show that intraclick interval varied from 0.4 to 0.7 msec during a single run. Doubling tends to disappear at high repetition rates, but otherwise there seems to be no sequential relationship to its occurrence, or to the length of intraclick interval, in our tests. Interestingly, doubled clicks recorded from Tursiops gilli at sea, off the California coast, show that if half of such a click is considered it appears identical with recorded examples of single clicks.

Frequency. The size of the largest sphere (6.25 cm) represents the wavelength of sound in sea water (20° C) of 23.8kHz. Since echo strength in water drops off sharply for objects below the diameter of a wavelength, it is likely that most of the information used by the discriminating animal in these tests was obtained from frequencies higher than our recording system could detect.

Even though in these runs we only examine the low frequency end of each emission it is evident that the animal exerts considerable control over the frequency composition of its signals. This control was evident when the animal switched from discrimination click emission to orientation click emission, after leaving the lever array (Fig. 1). While frequencies below the 2400-4800 Hz octave band were wholly absent in discrimination clicks they were well represented in orientation clicks down to the 300-600 Hz octave band.

Although recording gear with high frequency capability was not available during the discrimination tests it has subsequently become available. Additional studies of the same porpoise have been performed in which she was required to make one of the same blindfolded discriminations (3.18 vs 6.35 cm). Recordings made during this test allow sampling of the frequency range in her clicks. The apparatus consisted of an Ampex FR1300 tape recorder, with a tape speed of 60 ips, an Atlantic Research LC 32 hydrophone, and a Hewlett-Packard 466-A AC amplifier. The frequency range used by the porpoise in this discrimination was surprisingly low, with the approximate upper level at about 80kHz, and with the majority of energy concentrated between 16-30kHz.

Reverberations. Griffin (1955) has emphasized the difficulties in interpretation of sound in a reverberent aquatic situation, and rightly so, but the problems may be ours and not the porpoise's. Use of reverberation by the animal seems especially likely for the long-duration clicks, which because

of their length and low frequency content, generate much more reverberation than the short-duration higher-frequency discrimination clicks. A "ringing" of the environment develops (audible on the tapes), which is possibly quite useful to the animal in terms of the general placement of surrounding objects.

Echoes. Assuming our animal was using echoes from the spheres in its discrimination behavior, as seems likely, we may ask what information thus became available to the animal. Such information can be expected to fall into three categories. First, echo strength might be involved. Second, frequency composition of the echo is likely to be involved, and finally, the overall intensity pattern of the echo may be significant.

We made no analysis of echoes returning to the porpoise from the test spheres. However, we are fortunate that careful studies of echoes returning from submerged metal spheres have recently been reported (Hickling, 1962, 1964; Hickling and Diercks, 1966). These authors show that a metal sphere (12.7 cm in diameter), either hollow or solid, water or vacuum-filled behaves in part as an elastic and partly rigid object, and that its echo characteristics are predictable. Such echoes have been described by Hickling (1964) as follows: "The first point to note about the echoes is that, in each case, the first part corresponds to a rigid-body reflection, i.e. it has the same shape approximately as the incident pulse and has a travel time which shows that it has originated from the region on the surface closest to the source of incident waves. The remainder of the echo consists of sound generated by the vibrations induced within the sphere. For short incident pulses these secondary echoes are separated from the primary echo. For long pulses they overlap and interfere with the primary echo."

Since the initial part of the returning echo is a rigid body reflection,

and closely approximates the form of the impinging signal, a calculation can be made for the relative intensity of this portion of the signal for different spheres sizes. It proceeds as follows:

The signal strength (T) returned from an ensonified sphere of known dimensions and composition, in water, may be defined as:

$$T = 20 \log (P_s/P_i) \quad (1)$$

where P_i = the sound pressure incident upon the target, and P_s = the sound pressure scattered back at a distance of 1 m from the effective center of the target.

As an example, the target strength of a perfectly reflecting sphere of radius a meters, which theoretically reradiates the intercepted sound energy uniformly in all directions, is given by:

$$T = 20 \log (a/2) \quad (2)$$

This is the case for a perfect reflector, however if the target is not a perfect reflector, part of the energy intercepted by the target is converted to heat or into internal waves and only a fraction μ , of the energy, is reflected. The effect of absorption of sound by the target is therefore equivalent to reducing the target area by the fraction:

$$(1 - \mu) \quad (3)$$

The percentage reflectivity of the nickel-steel targets used in this experiment cannot be determined exactly, since an accurate value of the characteristic acoustic impedance ($\rho_o c_o$) of the steel used is not available. However, using the values for Steel 0.08 and 0.38 given in Olsen (1960) and Kinsler and Frey (1964), $\rho_o c_o$ steel = 390×10^4 and for sea water, 15.5×10^4 , the coefficient of sound power reflection α_r can be determined by the following equation:

$$\alpha_r = 1 - \frac{4\rho_o c_1 \rho_o c_2}{(\rho_o c_1 + \rho_o c_2)^2}$$

where $_{o}C_1$ = characteristic impedance of sea water 15.5×10^4 MKS rayls.

$_{o}C_2$ = characteristic impedance of steel 390×10^4 MKS rayls

by substituting the appropriate values, an α_r for steel of 0.96 is obtained.

Since $\alpha_r = \mu$ (i.e. fraction of energy reflected), the target area of the steel sphere used is effectively reduced by $1 - 0.96$ or 0.04. Relative target strengths for the range of spheres used in this study range from a difference of 6 dB for the greatest disparity to 1 dB for the smallest (5.71 cm vs 6.35 cm). Thus there is reason to expect that target strength of the initial echo may have contributed to the animal's size discrimination capability.

The effective size of the target also influences the frequency composition of the echo. For wavelengths of sound long in relation to the target area of the ensonified sphere reflection is small. As wavelength λ , approaches the value of the target area of the sphere, echo strength increases sharply, allowing a definition of the lowest frequency that one may expect to be strongly represented in an echo. The relationship is:

$$\sigma = \pi d^2/4 \quad (5)$$

where σ = target area, d = diameter of sphere

The energy content in signals reflected from rigid spheres of $d = 6.35$ cm, 5.71 cm, and 5.18 cm should be reduced at frequencies below 12.5kHz, 15.0kHz and 16.5kHz respectively. These differences are sizeable and would be expected to be easily detectable by the animal.

Finally, the secondary echoes found by Diercks and Hickling (op. cit.) result from the elastic nature of spheres suspended in water. These authors found very strong frequency-dependent pressure amplitude peaks and nulls in the echoes of their spheres, and were able to predict their position mathematically with remarkable fidelity. Their solid spheres acted much as if the sound was behaving as a surface wave within the sphere, and falling off toward

the interior. Echo forms were clearly dependent upon the nature of the reflecting material. For example, Hickling (1962, p. 1587) says: "In all cases the results begin at low frequencies as though the solid were a rigid body, changing in general into a fairly regular series of peaks and minima as frequency increases. With a rigid, incompressible material such as beryllium, the change from the rigid body solution is not very great. However, as the material becomes more compressible and pliant, the resonances tend to become more pronounced and more closely spaced. In the case of Lucite and ice the resonances have become quite sharp and close together." Armco Iron tested by Hickling falls about midway between the extremes, and supports well-defined resonances. Furthermore, Hickling showed that slight changes of dominant frequency in the incident pulse (as for example between 120kHz and 123kHz) could produce very marked differences in echo form, depending upon the constituent material.

Thus, when the porpoise ensonifies spheres with its echolocation clicks there would seem to be ample means for it to determine not only size but composition as well from the echo (Fig. 9). The first portion of the echo, where the size-dependent frequency roll-offs and intensity variations are found, could carry information about size. Information related to both composition and size could be carried in the later portions of the echo where the characteristic arrangement of nulls and peaks and pulse-length effects are most evident.

Discussion

When one requires a porpoise to indicate which of two ball bearings is larger by performing an instrumental act, one is really asking two questions: (1) Are the bearings of different sizes? and (2) which is larger? Our subject gave some indication that these two questions were real and separable to

her by occasionally turning abruptly away from the levers and stimulus array when the control test of two identical 6.35 cm spheres was presented. This behavior puzzled us for some time as it seemed inconceivable, at first, that an animal should be able to tell when this impossible problem had been presented and yet, at other times, know that a possible but difficult problem had been presented. In the latter case she often lengthened her decision-making time and still failed to choose the correct lever to press.

However, when one delves into the sort of information that may be carried in echoes from ensonified spheres it becomes evident that guideposts exist that might be difficult to sort out in a directional manner. Thus a single click from her might ensonify both spheres and if they were of different sizes, return to her with a mixture of two different lower frequency limits, and different intensities. Thus she might know that a problem was before her, but find its solution difficult.

It should be noted that it is only probably the case that the animal was making a direct assessment of sphere size in this experiment since a variety of other measurements varying in the same way as sphere size, could conceivably have been used. The discrimination of dimensional differences remains, however. The most likely object against which relative measurements could have been made was the presentation T that held the bearings. The amount of reflected sound from the presentation rod (9.5 mm diam.) was considerable but since it was symmetrical it should not have entered the size appraisal as a variable. For the animal to measure the dimensions of the spaces between the supporting rod and the inner surfaces of the bearings would seem to be a vastly harder problem than simply measuring the size of the spheres themselves. Similar measurements of the varying distances between the spheres and the water surface or the back wall, more than a meter away, seem even more remote.

It is evident that the porpoise exerts considerable control over several features of its signal output. It obviously can regulate repetition rate, intensity and frequency content and may have control over click-doubling. It is perhaps noteworthy that on slowed tapes at the end of long click trains one can often hear doubled clicks become increasingly well-defined, as if the intraclick interval were lengthening. It seems possible that all of these features may be interrelated and controlled by the state of the animal's sound producing mechanism. In the same way, orientation and discrimination clicks may be the generically-related ends of a continuum of possible signal variation. If the sound production depends upon the passage of air between vibrating tissue surfaces, as has been suggested (Norris, 1964) both changes in the tensions of the tissues and changes in air pressure would change several features of the generated signals. One can demonstrate this relationship by pressing one's lips tightly together and forcing air out as a stream of small bubbles which produce clicks not unlike those of a porpoise. Tightly pressed lips produce sharper, shorter signals, rich in high frequencies, and higher air pressure will speed repetition rate while also making some contribution to higher frequency content as well. Thus low-frequency-rich clicks are not produced by lips in high tension, and neither are the lowest repetition rates. Click doubling could also be related to pressure and tension. It seems to disappear at high repetition rates and in signals with the highest frequency content (for example those of Steno bredanensis; Norris and Evans, In press). Thus, it might be related to more modest tensions and pressures, which are especially evident toward the end of click trains, presumably just before a recycling of air is needed in the closed phonation system of a porpoise. If such an integrated system exists for the

various parameters of porpoise echolocation signals, then it will be most interesting to see what degree, if any, of independent control the animal possesses, of say, repetition rate and frequency composition.

Finally, some mention should be made of possible ways in which the porpoise uses the time relations within click trains to derive information. The rate-change of repetition rate itself can become a measure of gross closure rate at very close and moderately distant range. A much more precise measure is the time interval between the end of an outgoing click and the onset of its echo. Knowing its own speed within reasonable limits the porpoise should be able to gain a good idea of the relative speed of its target by assessment of the rate of change of echo placement. This very likely takes place not as an individual assessment of one click in relation to its echo, in rapid click trains at least, but as a psychoacoustical sensation produced by many clicks and echoes in which some features, such as the "difference tone," discussed by Nordmark (1960) provides the information. In this scheme the frequency of the tone would indicate distance, and the change in frequency the change of relative position between porpoise and target.

When a porpoise is inspecting its environment for information concerning composition of objects ensonified by its clicks, much or all of the elongate echo thus produced may be important. Thus the maintenance of a sufficient interspace between clicks to contain this echo may be important; implying that either click duration or repetition rate may be manipulated for this purpose.

Finally, discrimination clicks are short, with very rapid rise-times and have rather little energy at low frequencies, and in the case of the rough-tooth porpoise at least, they are highly directional. They thus

generate only minimal reverberation. Thus the switch from a discrimination click train to an orientation click train allows the animal to control reverberation to some degree, and also to ensonify a discrete target or much of the immediate environment.

Reverberations generated by the animal probably allow a quick general appraisal of the position and size of large objects during navigation. The placement of much energy in the low frequencies will allow such signals to function at greater range than discrimination signals. They may find use in localization of distant schools of fish or porpoises, of ships and of the general topography of the bottom. It is suggestive that many of the signals recorded at sea in genera such as sperm whales (Physeter; see Backus and Schevill, 1966), pilot whales (Globicephala; pers. obs.) and false killer whales (Pseudorca; pers. obs.) have been of this type.

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Abstract

An Atlantic bottlenose porpoise was required to discriminate between two sizes of nickel steel ball bearings presented underwater, by pressing one of a pair of levers, on the side of the largest sphere. Performance was perfect at disparities of 5.40 vs 6.35 cm or greater, and fell to 77% success at a disparity of 5.71 vs 6.35 cm. During these tests the blindfolded subject circled in the tank, respired once at about midtank, and began a continuous emission of clicks as she swam toward the choice levers. Emitted signals were recorded during different disparity levels. Click trains usually started with a high repetition-rate burst and quickly descended to rather constant levels between 50-70/sec until just before lever press when repetition rates rose to 130-180/sec. A silent period often just preceded lever press. Following the press the animal emitted about a dozen very intense low frequency-rich clicks which we have termed orientation clicks.

Echoes almost always fell in the interclick interval and it is postulated that a "difference tone" is being used to determine closure rate. Determination of sphere size and disparity may have depended upon three factors; size-related frequency roll-offs, echo intensity, and ringing induced by the ensonifying click. Double clicks were often used, and other evidence for control of features of signal output are given.

DISCUSSION

by

Dr. D. BATTEAU

Dr. Norris's paper, regarding the use of sound by a dolphin to discriminate between objects, is particularly interesting because of the pioneer nature of the investigation. It provides an accurate documentation of ability which gives substance to behavior which dolphins have been reported to exhibit frequently. The experiment described also poses, or brings again to attention, the question of means employed by the animal accomplishing the recognition.

Trainers working with animals are aware that the intended training cues provided and the unintended cues accompanying their activity are not directly separable by an animal. As the inadvertent behavior of the trainer is consistent with the training activity, the wrong conclusion can be drawn concerning the animal's actions. The animal may be responding to signals of which the trainer is completely unaware. In the reposted experiment, however, the possibility of mistaken interpretation seems to have been adequately avoided and the results can be correctly attributed to discrimination in sound.

We then may ask, as Dr. Norris did, what characteristics of the sounds are the dolphin using in discrimination. In this regard the question of equipment characteristics always arises because of the severe requirement that animal sounds are to be investigated, not gross distortions of animal sounds by reason of equipment limitation. Only when it can be certain that the true sounds are available can the decision be accurately made, and this requires adequate bandwidth in frequency, and adequate dynamic range in volume. The lack of the former creates false spectra or misleading oscillograms, and the lack of the latter deletes important characteristics from the recording and adds confusing information regarding the equipment.

We may consider the problem from the viewpoint of the communications

engineer and call the sound received from objects and environment a message. The task of the dolphin in the situation described is to understand a particular part of that message having to do with the solid objects of the experiment. He must be able not only to assess their sounds but also to separate those sounds from others resulting from reverberation, water noise, or other sounds present in the environment. This is substantially the problem of receiving an intelligible message through a noisy channel.

This leads us to inquire regarding the necessary characteristics of a channel which will provide the required message and also into the nature of the noise and means of ignoring it. If we turn mathematical for a moment, we can apply ideas relating to geometry as developed by David Hilbert ("Foundations of Geometry"; "Mathematical Physics") . From the geometrical point of view, the environment is three dimensional, and any channel capable of describing it must have the possibility of providing three dimensional messages. When the reference point, or origin, is not fixed, as is the case with a moving animal, at least four independent subchannels are needed, one to provide a reference or origin and three to indicate values on the three coordinate lines. A set having the required dimensionality is called a spanning set or simply "spanning" and if it has exactly the required number of elements it is called a basis.

With this mathematical requirement we can ask regarding the means of providing a suitable spanning acoustically. Clearly such a set could be developed in a number of ways. If a single tone is used as the illumination, then the animal must occupy successively four different positions which must give three independent planes so as to map the surrounding space onto a suitable acoustical frame. If the animal is stationary or moving

slowly, the characteristics of the sound must be different from a single tone and must itself provide a spanning. Examples of spanning sounds are (1) pulses or sharp clicks, (2) noise, (3) tones with harmonic structure, and (4) frequency sweeps.

Although each of these classes of spanning sounds appears to have application by some animal, I would like to direct our attention to the spanning class "pulses". The means by which I speak to you is an excellent example of its employment. The vocal pulses are reverberated in the vocal tract, which is rapidly modified to provide a time sequence called "spoken English". If any question of feasibility were to arise, it seems to me that this example is sufficient to settle it. Not only spoken English is recognized, but usually subtle differences sufficient to identify one speaker out of thousands are encoded by the speaker and recognized by the hearer. Of course, if I were to whisper, the class "noise" would be represented and would also provide recognizable messages. However, speech cannot result from a pure, continuous tone.

If having directed attention to the use of pulses to write sonic messages, we consider the pulses produced by the dolphin, it is easy to consider recognition by this means. When we examine dolphin pulses carefully, we find that the rise time is a microsecond or less, which requires a bandwidth of approximately 160 kHz if the information capacity of the channel is to be preserved. Fortunately, the experiments of Dr. Johnson show that at least one Tursiops truncatus can hear to 150 kHz so that the utilization of most of the channel seems likely.

This, however, presents severe requirements on equipment for general use in investigation of dolphin pulses. In Dr. Norris's experiment, the full channel may not have been required for the sounds from the objects. As he said, it should be well recognized that the recording equipment used

did not present the complete channel, so that attempts to find the message characteristics from those tapes could very well be difficult or impossible. If we inquire as to the frequency range of resonance, or ringing, from the objects employed, it is conceivable that the records would barely contain some of the significant data.

Looking at the writing of messages in a pulse channel generally may be of value. When I speak of "channel" in this manner, I do not refer to wires or hydrophones, but to the symbolic structure and its patterns, as in regarding the alphabet as a channel for written language. The pulse obviously provides the basic code element, and its characteristic iteration by various paths, or the reverberation of the environment or object, provides the message. This is a basic PPM (pulse-position-modulation), form of encoding. There is an additional factor which may be called "coloration", which is the alteration of the spectrum of the pulse by the characteristic of material from which the pulse is reflected. The basic channel is then PPM + coloration. If attention is paid only to the coloration and not to the position, basic information is drastically lost. This consideration may provide an emphasis to the remarks of Dr. McKay which point out the need to preserve phase information in animal sounds.

When we recognize the bandwidth available to the dolphin, and compare it with the bandwidth available to the ordinary man of about 10 % of that of the dolphins', we can point out the error of "trusting your ears" in listening to the dolphin sounds. This holds true even when the tapes are played at one-quarter speed. The speed reduction should be 16 to 1 if characterizations are to be retained. This also supposes that the original information was in part recorded. We should then also be quite aware of the possibility that sounds identical to the human hearer could be widely different to the dolphin. These remarks are to direct attention to the "unknown but not

unknowable" communication.

The "unknown but not unknowable" communication is exemplified also by the unrecognized cues in training and experimental situations. While we can state accurate mathematical requirements regarding "messages" and "spannings" it remains for careful research, of which Dr. Norris has provided us an example, to demonstrate the realization of conditions, and hopefully to point to data for decision among the many possibilities as to which one is in use, including which sensory channel is the significant one. That is to say, we examine not only the meaning of the message, as exhibited by behavior, but also look for the alphabet and logic of encoding, using adequate equipment, to know the true nature of animal sounds and behavior.

DISCUSSION

by

A. D. GRINNELL

Although I originally had no intention of saying anything about this, I feel that the discussion has drifted sufficiently far in its consideration of how dolphins hear, to justify my introducing some experimental evidence to spice the speculation. I refer to experiments performed during December of 1965 in Ito, Japan, in collaboration with Prof. T. H. Bullock and Prof. Y. Katsuki and his associates. Using techniques of anesthesia recently developed by Nagle, Morgane and McFarland in Miami, and Ridgeway at Pt. Magu, we anesthetized dolphins of the genus Stenella and recorded from several auditory centers, particularly the posterior colliculus and the superior olivary nuclei. These locations were found by rather crude stereotaxic guesswork based on previous dissections, but yielded responses consistent with the expected nuclei, and histological work subsequently confirmed that we were

where we thought we were. We used 15 cm. long sharpened tungsten wire electrodes, insulated to the tip, inserted through a hole drilled through the dorsal surface of the skull and then through the bony tentorium overlying the colliculus. Actually, the electrode was lowered through a metal tube (an umbrella strut, I believe) that served as a wire guide. This electrode recorded evoked potentials to air-borne sound presented in the form of brief ultrasonic tone pips. The results important to this discussion concern the sensitivity to sound of different frequencies directed perpendicular to different points on the surface of the animals' heads. A 5 cm. diameter loudspeaker held a few cm. away from the surface provided a reasonably localized stimulus. At low frequencies (15-30 kc), this stimulus was quite effective when directed toward the external ear, but slightly more effective when aimed at the side of the lower jaw or just to one side of the front of the melon. At high frequencies (50-100 kc) or with clicks, sensitivity was greatest to sound directed at the side of the lower jaw, only slightly less to sound directed at the contralateral side of the melon, and much reduced to sound aimed at the external meatus. Thus, as Norris has suggested, the lower jaw does seem to be capable of serving an important hearing function. To the best of my knowledge, the pathway via the melon was unexpected. Clearly, in both cases, sound energy is having its effect through the cochlea and normal auditory neural pathways. Whether it uses the middle ear apparatus in both cases is less certain, but it perfectly well could, despite the isolation of the bullae from the skull. Sound could travel very effectively through soft tissue channels. Obviously these experiments must be repeated with water-coupled stimuli, where the effective energy will be much greater and the importance of angle of incidence reduced. This we hope to do in the coming year.

DISCUSSION

par

J. L. NICOLAS

1.- Il est certain que la classification et l'identification d'un objet posent des problèmes bien plus difficiles que son repérage; la quantité d'information à manipuler y est infiniment plus grande et son traitement plus subtil. Aussi la "reconnaissance des formes" est-elle encore assez loin d'être résolue malgré les efforts variés de nombreux chercheurs.

L'étude de K. NORRIS, W. EVANS et R. TURNER est particulièrement intéressante pour nous ingénieurs, car elle présente une nouvelle approche de ce problème complexe, et je pense que celle-ci est extrêmement riche en elle-même, et devrait fournir de nombreuses pistes à explorer. Etant donné ses possibilités on aimerait qu'elle fut commencée depuis plus longtemps; les résultats présentés par les auteurs ne font que renforcer cette opinion.

2.- Comme l'indique les auteurs le rerayonnement d'une sphère métallique est bien étudié sur le plan théorique; les travaux d'Hickling permettent de formuler quelques hypothèses sur le procédé utilisé par l'animal pour faire la discrimination des 2 cibles qu'on lui présente.

Il s'agit de déterminer expérimentalement quels sont les paramètres de la cible qui fournissent l'information.

En ce qui concerne l'hypothèse d'une classification faite par une mesure de l'index de réflexion lié au seul rayon de la sphère, il semble que l'on pourrait aisément l'infirmier ou la confirmer.

Si l'animal se place à une égale distance des 2 sphères d'épreuve il peut en effet par une simple mesure comparative de niveaux sonores reçus déterminer la plus

grosse des deux, c'est à dire reconnaître la sphère étalon, à condition toutefois que les 2 sphères soient faites avec le même matériau.

On peut interdire à l'animal cette possibilité en lui présentant des sphères d'épreuve réalisée en matériaux différents, qui auraient soit le même diamètre, mais alors des index de réflexion différents, soit des diamètres différents, mais des index identiques.

Le comportement de l'animal placé devant un tel couple de sphère pourrait être instructif.

Il semble aussi qu'une observation fine des positions successives de l'animal au cours de sa recherche, et des orientations de son museau, pourrait fournir des renseignements intéressants.

La nature nous présente habituellement des solutions assez sophistiquées, et il serait étonnant qu'elle se soit contentée d'avoir créé pour le dauphin un appareil de simple mesure de niveau sonore. D'ailleurs il semble bien que cet animal soit capable de distinguer entre elles des formes plus compliquées, pour lesquelles une mesure énergétique soit insuffisante.

3.- Il apparait que le dauphin serait capable d'exploiter à son profit la réverbération créée par ses propres émissions. Ceci serait tout à fait remarquable car, nous, faute de savoir utiliser le phénomène de réverbération, nous nous efforcerons de trouver des modes d'émission et de réception nous permettant de réduire les effets nuisibles de celle-ci.

C'est pourquoi la tendance actuelle est d'utiliser des signaux à large bande qui, sur le plan théorique, sont intéressants pour d'une part lutter contre la réverbération, d'autre part obtenir des pouvoirs de résolution élevés.

Si on suppose que le détecteur du dauphin effectue un traitement cohérent utilisant un "filtre adapté", la performance contre la réverbération ne dépend que de la

largeur de bande B du signal, et le pouvoir de résolution en temps est de l'ordre de $\frac{1}{B}$.

Une question se pose alors: la largeur de bande provient-elle uniquement de la durée, ou bien d'une certaine modulation en fréquence ?

Si on pouvait utiliser un système expérimental réduisant la réverbération, on pourrait mettre en évidence une modification, ou une absence de modification, de la largeur de bande des signaux, et ainsi préciser son exploitation.

4.- La théorie de Hickling montre qu'il existe une fréquence à partir de laquelle la puissance du début de l'écho tombe, toutes choses égales par ailleurs, pourrait-on montrer que l'animal recherche cette fréquence ?

5.- En ce qui concerne la directivité de l'émission du système sonar du dauphin, la seule lecture de ce travail ne permet pas de conclure sur sa finesse. Il serait important de savoir si l'animal "interroge" simultanément, ou séparément les 2 sphères.

On pourrait aussi songer à interdire à l'animal d'insonifier simultanément les 2 sphères, et le placer ainsi dans les mêmes conditions que l'on rencontre lorsque l'on a à distinguer des jumeaux non placés côte à côte. L'animal fait-il une mesure absolue, ou une mesure relative ? Cette question pose finalement celle de la nature de la mémoire de l'animal, elle déborde du cadre du travail présenté, mais peut-on aborder les problèmes de classification en ignorant ceux de la mémoire ?

6.- Ce qui apparait nettement et finalement ce qui est le plus remarquable, c'est la capacité d'adaptation du sonar du dauphin à des situations très variées.

Cette faculté est-elle seulement liée à la multiplicité des cellules concernées par ce mécanisme d'écholocalisation, ou bien relève-t-elle d'un autre principe qu'il

serait très important de préciser ?

7.- Pour conclure ces commentaires, je suis obligé de constater qu'en fin de compte c'est une série de questions qui m'est venue à l'esprit à la lecture de cette communication tout à fait passionnante. Je ne prétends pas avoir ici, loin de là, fourni une liste exhaustive, d'autant plus que j'imagine qu'il existe déjà des réponses à certaines questions ou que des expériences déjà commencées devraient apporter d'autres réponses.

C'est finalement un dialogue qui est ici amorcé, entre le biologiste et l'ingénieur, et l'un des mérites du colloque, et non le moindre à mon avis, c'est de permettre de le poursuivre.

IV

Résistance aux signaux interférents

Resistance to interfering signals

MECHANISMS OF OVERCOMING INTERFERENCE IN ECHOLOCATING ANIMALS

by

Alan D. GRINNELL

Echolocating animals display extraordinary sensory capabilities in detecting faint echoes, determining the distance and direction of the echo source, and discerning the nature of the target (Griffin, 1958; Grinnell, 1962; Griffin, Friend and Webster, 1965). Electro-physiological studies of audition in bats have revealed neural adaptations that go far toward explaining these abilities (Grinnell, 1962, 1963a-d; Grinnell and Grinnell, 1965; Suga, 1964a,b; 1965a,b; Henson, 1965); but little consideration has yet been given to the most serious problem of all, i.e., that bats--and other echolocating animals--must be able to perform these extraordinary sensory analyses under seemingly impossible conditions of interference. It is my intention to review here some of the more obvious forms of interference that echolocating animals face and to consider possible ways in which these problems might be overcome. Since most of our knowledge both of the skills of echolocation and possible mechanisms of neural processing to permit them come from studies of bats, I will use these remarkable animals as my main subjects throughout, particularly the little brown bat, Myotis lucifugus, and the long-eared bat, Plecotus townsendii. It is necessary to caution at the outset, however, that by the very nature of the topic much of what follows can only be labeled speculation.

Major sources of interference.

The first major source of interference is the outgoing pulse itself. Since sound in air travels more than a foot per msec. (34.4 cm/msec.),

an echo must be heard and analyzed very soon after the onset of the outgoing cry. Most bats appear to shorten their pulses enough during approach to a target that there is no actual overlap, the echo always falling in a "silent" period; but some bats have pulses of longer duration, where overlap is almost inevitable, and even in those species where the echo falls in a silent period after the outgoing pulse, the interval will be so short for close objects that one would expect the auditory system to be refractory following response to the louder outgoing pulse. This problem is accentuated in aquatic echolocating animals, where the speed of sound is nearly five times that in air.

A second and probably more serious form of interference is the nearly simultaneous return of echoes from many different targets. The arrival time, intensity and frequency content of each echo must be independently analyzed, since they reflect the distance, shape and direction of the targets, most of which are probably of importance to the animal (e.g. obstacles such as leaves, tree twigs and branches, wires, buildings, etc., in the animal's path or targets at any angle that might represent possible meals).

At the same time, most echolocating animals, being gregarious, face interference from the outgoing orientation sounds of companions and the reflected echoes of these cries. Although it is conceivable that such extraneous orientation sounds might be useful to an animal capable of analyzing echoes of similar but self-emitted cries, it seems more likely that these sounds are of no value in echolocation and must simply represent "jamming" noise.

Finally, there exists the wide spectrum of ambient noises in an animal's environment, some of which might represent important sources of information (e.g. an insect's wing-beat sounds), but most of which are probably only "noise" that must be heard through. By employing ultrasound bats have avoided much of this ambient noise,

but the problem still presents itself in such sources as wind whistling through vegetation, rushing water, and ultrasonic insect noises. The only really quantitative assessment of bat ability to resist interference has been made with such "ambient" noise, in experiments designed to "jam" bats with broad-band white noise under controlled laboratory conditions (Griffin, McCue & Grinnell, 1963). In these, the long-eared bat, Plecotus townsendii, was found to detect echoes that were near, if not beyond, the limits of detectability set by information theory. A more detailed consideration of these experiments will follow.

It is obvious that resistance to interference from all these sources depends principally on two capabilities: (1) a high degree of precision in discrimination of echoes of self-emitted sounds from other sounds, and (2) extraordinary temporal precision: the ability to separately analyze and place accurately in space all of the prominent returning echoes, even when they occur nearly simultaneously with considerable overlap.

Recognition of meaningful echoes.

A careful analysis of emitted sounds has been done with very few species of bats, but where it has been, notably in bats employing FM pulses or constant wavelength signals with several harmonics, it has been found that there are detectable slight differences between successive pulses emitted by the same bat or between pulses emitted by different bats. These may differ in duration, rate and pattern of frequency change, onset and termination frequency, repetition rate, and intensity pattern during emission. All but intensity pattern

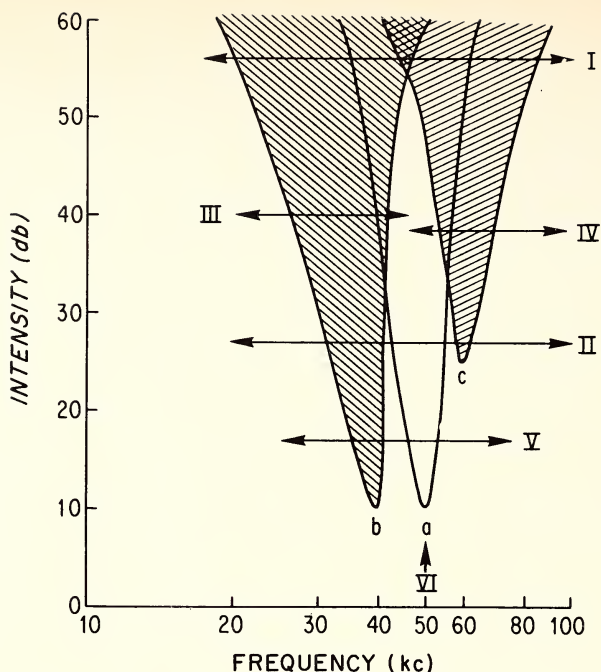


Fig. 1. "Tuning area" diagram of a hypothetical collicular neuron based on response patterns described by Suga (1965a,b) and showing how cells can be used to analyze echo characteristics. The cell has an excitatory input, a, bordered by inhibitory inputs from other cells, b and c. If it is assumed that the excitatory and inhibitory inputs have the same latency and that the inhibition lasts several msec, then a tone pip at the units best frequency (VI) will excite only at intensities lower than 55 dB. A long FM sweep in either direction between intensities I and II will give no response. The upward sweep shown in line III would not elicit a response, but a downward sweep though the same range would, while the opposite is true of sweep IV. A lower intensity FM sound (V) would be excitatory only if swept downward in frequency. Responses, when present, would be expected to be highly phasic. If the inhibitory inputs were of longer or shorter latency than the excitatory input, the effect of sweeping in different directions or at different rates would be profoundly different, and equally important changes in response pattern could result from having extremely short-term inhibition.

will be faithfully reflected in the returning echo, while changes in intensity pattern are important in themselves as clues to target dimensions.

There is good evidence that the neural capability exists for performing the analyses necessary for such recognition and target discrimination. It has been found, for example, that bats are capable of extremely accurate frequency and intensity discrimination. At the level of the colliculus, many single units exist in all areas of the frequency spectrum that have extremely sharp "tuning curves," with excitation restricted to a 2-5 kHz bandwidth sharpened by inhibition at higher and lower frequencies. The resulting changes in sensitivity may exceed 10 or 20 dB for a one percent change in frequency (Grinnell, 1963a, Suga, 1964a). At the same time, a significant number of collicular cells are capable of intensity discriminations as small as 0.2-0.5 dB (Grinnell, 1963a). Other cells show sharp changes in threshold or firing pattern with changes in duration of a signal, especially in the range 0.5-1.5 msec (Grinnell, 1963b). Perhaps most important, however, are the large numbers of cells found in the colliculus and cortex and studied in elegant detail by Suga (1964b, 1965a,b) that respond in a way determined by the intensity and rate, extent, and direction of sweep of FM sounds. These are usually units with a narrow excitatory response area bordered by inhibitory areas of lower or higher threshold that can inhibit at different delays and for different lengths of time, so that a frequency sweep in one direction may result in a response while in the other direction or at a different rate it will not. Fig. 1 shows a hypothetical cell similar to many described by Suga, and some of the many possible

ways in which such a cell could "recognize" fine details of a signal. A few cells have been found in the colliculus and more in the cortex that have lower thresholds to FM sounds than to any constant wavelength (CW) sound (Grinnell & McCue, 1963; Suga, 1965a,b).

The existence of cells with the above behavior is probably sufficient to account for a bat's ability to discern differences between its own and other bats' cries, and even its own successive pulses, to assess differences in returning echoes reflecting target dimensions, and to make the binaural comparisons of echo intensity at different frequencies that may be necessary for target localization (Grinnell and Grinnell, 1965).

In order for this discriminating apparatus to be of value, however, it is necessary that the bat know the characteristics of the echoes that will prove meaningful, that is, be able to recognize echoes of its own immediately preceding emitted pulse and distinguish them even from echoes of its own earlier pulses. One must postulate the existence of cells, in the cortex, perhaps, that can assess the firing pattern of more peripheral populations (their input) and recognize these patterns as belonging to a meaningful echo or not, representing an obstacle or a potential meal, a tasty or distasteful insect, etc. This recognition probably depends on a short-term "memory" of the characteristics of the emitted pulse, just heard. Evidence of such short-term "coding" of the auditory system is clear even at more peripheral levels, where large populations of cells are transiently "sensitized" to a second sound having the same characteristics as the first. Single units in the colliculus are commonly

as much as 15-20 dB more sensitive to the second of two identical tone pips than to the first and some cells respond only to the second of two such identical stimuli. This facilitation lasts only 10-20 msec and is obvious even in the evoked potentials, especially the prominent potential (N_4) representing input to the posterior colliculus, in which the response to an identical second stimulus may be 50-100% greater than the response to the first (Grinnell, 1963b). The facilitation is correspondingly less for second sounds progressively removed in frequency (Grinnell, 1963d). The present evidence for such "coding" is restricted to data obtained with tone pips. There is at present no convincing evidence that populations are coded to respond preferentially to sounds having the same duration or pattern of frequency change. Such populations almost certainly exist, however, especially in the form of cells "tuned" to respond preferentially to a sound having the same particular FM characteristics as the outgoing pulse just heard. If such specifically-facilitated populations do exist, then the problem of identification of meaningful echoes seems largely solved. The demonstration of such behavior, and of the change in firing pattern of different cells to very subtly differing, preferably natural, stimuli is unquestionably one of the next goals of bat neurophysiology.

Temporal Resolution Requirements

In order for echoes to be heard and independently analyzed, there must be an adequate number of receptor cells and higher integrative populations available at the appropriate time: cells either that have not fired to immediately preceding signals (outgoing pulse

or other returning echoes) or that have quickly recovered and can fire again. The size of the cell populations sensitive at any given moment depends principally on the number of cells firing to the previous sound at the same frequency (a function of the intensity of the preceding sound) and the time allowed for recovery (the interval since the preceding pulse).

Most bats emit extremely loud pulses, approaching the pain threshold, so that whatever the geometry of vocal cords, eustacean tube, and ear, there can be little doubt that they hear the outgoing pulse, probably much louder than any echoes. (Indeed, it is presumably necessary that the outgoing pulse be heard, if its characteristics are to be known and the auditory system sensitized to echoes having the same characteristics.) The repetition rate of these orientation cries typically varies from 10/sec to 200/sec in bats, up to 600 or more/sec in dolphins. Since echolocating bats normally fly at a speed of 2-4 meters/sec. and must have a minimum reaction time of 1/10 to 1/20 sec, they presumably cannot make use of echoes returning within approximately in the last 10 cm, i.e., within about 0.6 msec of the outgoing cry. In other instances, however, bats hover near targets, or locate targets while hanging stationary, in which case reaction time is not important and objects at less than 10 cm distance (less than 0.6 msec interval) can probably be detected and recognized. It is necessary, therefore, that we be able to explain the presence of significant numbers of sensitive elements even at intervals of less than 0.6 msec after the loud outgoing cry, to which most auditory neurons might be expected to respond.

This problem may not be as formidable as once envisioned, since

it is now evident, from the beautiful work of Henson (1965), that the middle ear muscles in Tadarida brasiliensis mexicana and presumably in other bats can and do contract just before and relax at the end of such emitted pulse, reducing sensitivity by as much as 10-15 dB during the outgoing cry. This protective mechanism is clearly of importance during "searching" flight, when emitted pulses are loudest and at lowest repetition rate. After detection, when the repetition rate rises sharply, middle ear contraction is more sustained and therefore much less selective in blocking out the emitted cry.

In addition to this middle ear blanking mechanism, it is quite possible that there is a neural equivalent inhibiting some fraction of the peripheral auditory activity during emission. This has not been sought or demonstrated yet, but could theoretically provide a much faster, more accurate means of reducing the effect of the outgoing cry.

Even more severe problems of temporal resolution arise from the nearly coincident return of many echoes. Normally a bat must be able to interpret a barrage of echoes from objects at about the same distance but in many different directions: tree twigs near the insect being pursued, a larger branch to one side, a telephone wire to the other...perhaps a total of 10-15 similar echoes arriving within a 4-5 msec period after pulse emission, each echo carrying unique information about the exact distance, dimensions, and direction of the reflecting object. Each echo must presumably be independently analyzed for all of these parameters. Yet the differences in arrival time will measure only 60 microseconds/cm difference in distance,

It is not possible to say how close together in time two echoes

can be resolved and used by bats. It is apparent that the problem a bat faces is increased when such resolution is necessary. For example, it has long been recognized that bats do better in wire avoidance if the wires are near the middle of a room rather than near a wall (Griffin, 1958). Under such conditions it is apparently difficult to resolve the faint echo from the much louder echo off the wall at 1-2 msec greater interval. Similarly, most bats, trained to catch mealworms in air in the laboratory, will not attempt capture if 10-15 mealworms are thrown up simultaneously. In this case the returning echoes would be of approximately the same intensity but very close together in time, since the mealworms normally spread to only a few cm distance from each other. Nevertheless, some bats consistently do single out one mealworm from such a group (Webster, 1963); and other situations almost certainly exist in which two echoes must be analyzed at only 100-300 microseconds interval. It would be most surprising if echoes arriving simultaneously from two targets could be distinguished from each other. Perhaps this is impossible even at separations of 50-100 microseconds. But at greater intervals than this, it seems probable that the ability exists. Behavioral determination of the shortest discriminable interval seems practicable, and would be of immense interest.

The duration of any given 2-5 kHz bandwidth within a typical Vespertilionid FM pulse is about 50-100 microseconds. In order for this frequency component in two echoes to elicit separate responses at, say, 200 microseconds separation, it is necessary that there be two distinguishable peaks of vibration of the appropriate point on

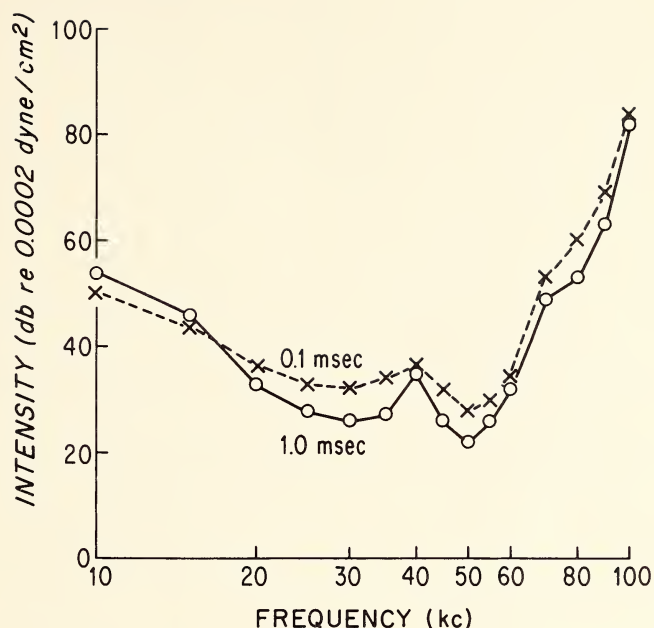


Fig. 2. Audiograms of the collicular evoked potential of the bat, Phyllostomus hastatus panamensis, showing the close similarity between curves made with a 1.0 msec tone pip (0.3 msec rise time and fall time) and with a 100 microsecond tone pip (50 microseconds rise and fall). Such similarities are typical of all bats studied to date. There are normally no differences between audiograms made with 1 msec or longer pulses having the same rise time. (Bat temperature, 36° C.)

the basilar membrane at this interval. No information is available specifically concerning the mechanics of the bat cochlea; but two considerations lead to some confidence that the peaks of vibration are sufficiently quickly established and sharply localized: (1) the observed accuracy of frequency discrimination (Grinnell, 1963a, Suga, 1964a), and (2) the extraordinary speed of pitch discrimination, evidence for which is seen in the close similarity between evoked potential audiograms made either with 1 to 10 msec or 0.1 msec tone pips (Fig. 2). Reasonably accurate discrimination of frequency seems to be possible with only 2-3 cycles of sound, perhaps less. If the basilar membrane is capable of the necessary resolution, then the principal requirement is for some small portion of the sensory elements at any given locus to be sensitive to each echo, even if most of them have just fired to the outgoing pulse or an earlier echo.

Recovery of responsiveness.

Perhaps the most dramatic specialization of the bat auditory system for echolocation is its phenomenally fast recovery of responsiveness, and particularly the central enhancement of recovery, apparent in Fig. 3. Discrete evoked potential responses to both of two tone pips are seen down to intervals of 0.4 msec, both at the auditory nerve and the posterior colliculus. As Fig. 3a shows, the interval required for full recovery of the auditory nerve response (N_1) is more than 10-20 msec on the average. This is only slightly faster recovery than is seen in other mammalian auditory nerves. In contrast to findings in other mammals, however, as the interval between stimuli is increased, responsiveness increases more rapidly at higher neural levels than in the auditory nerve under the same

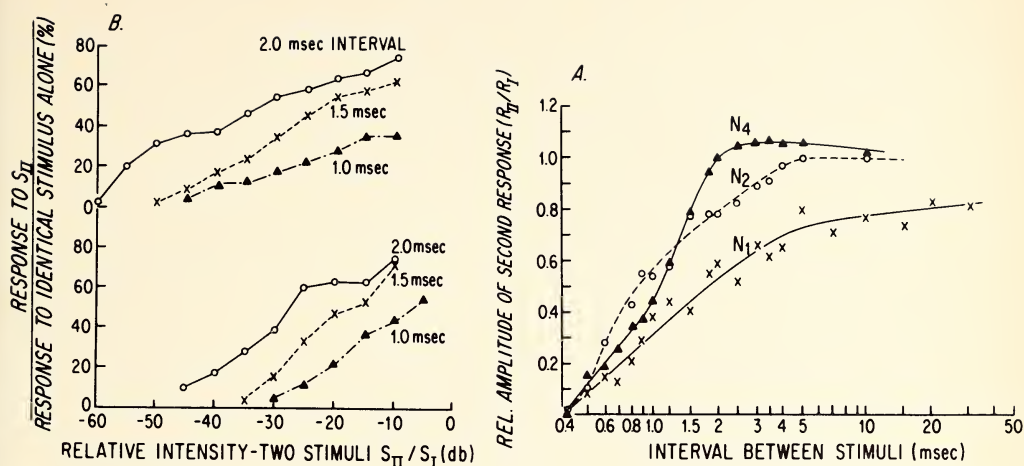


Fig. 3. A. Average recovery curves for the positive evoked potential representing activity in the auditory nerve (N_1), in the cochlear nucleus (N_2), and in the higher order input to the posterior colliculus (N_4) of Plecotus. Pairs of identical stimuli of 50 kHz or higher frequency and within 40 dB of threshold were presented at the intervals shown, and the response to the second of the two compared with that to the first. Note the enhancement of recovery between N_1 and N_4 (from Grinnell, 1963b).

B. Average recovery curves showing the response of N_4 and N_1 to the second of two high frequency (40 kHz or higher) tone pips identical in all respects except intensity. At 1.0, 1.5, and 2.0 msec interval, the responses to a second stimulus as much as 55 dB fainter than the first are compared with the responses to the fainter stimulus alone. The first stimulus was always 60 dB above threshold (Grinnell, 1963b).

stimulus conditions. Only 5 msec is required at the cochlear nuclei (N_2); while the input to the colliculus (N_4) is fully recovered, on the average, in only 2 msec, following which there is often a short period when the second response is larger than the first. A nearly fully recovered N_4 can often be seen when the N_1 is only 20-30% recovered. In short, there is a marked recruitment or exaggeration of response to a second stimulus at higher neural levels. The same phenomenon is seen when fainter second stimuli are used, there being considerable recovery at N_4 even when the first tone pip is 50-55 dB louder than the second, and N_1 shows very little recovery (Fig. 3b).

This acceleration of recovery at the second and third neural levels is explained, at least in part, by cell types that have already been mentioned: cells that are transiently sensitized by as much as 20 dB to a second pulse; others that will respond only to a second stimulus. Still others have been found that respond best to sounds repeated at repetition rates approximating those in a bat's "buzz," around 100-200/sec (Grinnell, 1963b; Friend, Suga, & Suthers, 1966). Such populations, added to the large number of cells that simply respond to both stimuli at intervals greater than a certain individual minimum, probably account for the apparent large increase in the fraction of the total cell population in a given nucleus activated by a second sound as one proceeds from the auditory nerve to more central nuclei.

It is also interesting to note in this context the large number of cells in the colliculus and cortex that respond only to faint sounds, having high intensity as well as low intensity thresholds (Grinnell, 1963a; Suga, 1965a; and see Fig. 1). In most such cells

the lack of response to loud stimuli is probably the result of inhibition that last several msec (Suga, 1965b), inhibiting response to echoes as well. On the other hand, it is easy to conceive of circuitry that would permit a high intensity threshold without long-term inhibition, leaving the unit responsive to a fainter second sound. Such cells, if they exist, would clearly constitute important "echo analyzers" and would contribute to central enhancement of recovery.

However great the "amplifying" power of the central nuclei, on the other hand, it is necessary to have a signal to work with. This signal, the information in the second stimulus (echo), must be present in the auditory nerve, where mechanisms for specific response to second or fainter stimuli have not been found.

Resolution at the first neural level.

As was indicated above, the bat auditory system must be responsive to an echo at intervals greater than 0.5-0.6 msec after the much louder outgoing cry, perhaps at shorter intervals in special cases. Multiple echoes, having more nearly equivalent intensities, must very likely be independently heard down to 100-200 microsec intervals. It is not obvious which of these requirements is the more stringent.

There is a minimum interval between presentations of the same frequency, either in separate tone pips or in overlapping FM sounds, for a detectable evoked potential response (Grinnell and McCue, 1963). This seems to be about 0.3-0.5 msec, depending primarily on the duration and intensity of that frequency in the first stimulus. This

is unquestionably an upper limit to the necessary minimum recovery time, however, since a large population of responding elements is necessary for a detectable evoked potential, and smaller numbers could perfectly well carry the necessary information. Good quantitative evidence for the efficacy of grossly "undetectable" responding elements is seen in the comparison of recovery at the auditory nerve (N_1) and the input to the colliculus (N_4) to second stimuli fainter than the first (Fig. 3b). When the second was 40 dB fainter than the first, for example, there was no detectable response, on the average, even at 1.5 msec interval at N_1 in Myotis, while at N_4 , there was a clear response at 1 msec interval. Obviously the information was present in N_1 , but at a level too low to be detected, even though the threshold and response amplitude of N_1 to the first stimulus were fully equivalent to that of N_4 . Similarly, at a given interval, a detectable N_4 is seen to a much (average 15 dB) fainter second stimulus than is necessary for a detectable N_1 , even though the information again has to be present in N_1 at this point 15 dB below gross detectability.

It seems not at all impossible, therefore, that N_1 should be transmitting useful information about echoes at intervals of 0.6 msec or less after an emitted pulse, or within 0.1 to 0.3 msec of another echo. The question is: what elements are responsible for this information? Large numbers of cells in the colliculus (Grinnell, 1963b, Suga, 1964a) and cochlear nucleus (Suga, 1964a) have been found to recover rapidly after responding, a few at intervals as short as 0.6 msec, and increasing numbers at 1 msec and greater

intervals. It is surely to be expected that the spiral ganglion has cells capable of as fast recovery. It seems reasonable to further postulate that most echo detection and analysis can be accomplished by such cells that fire to the emitted pulse, then after a characteristic refractory period, be it 0.6 msec or 10 msec, become capable of firing again. Differences in duration of refractoriness and absolute threshold can assure the existence of sensitive populations at any given time after a loud sound, except at intervals too short to permit any recovery. Probably a sufficient number of cells recover responsiveness within any given 100 microsecond period to assure echo discrimination under most circumstances.

In some cases, however, e.g. when a bat is hovering near an obstacle (with an important echo returning at less than 0.6 msec delay), or trying to discriminate a small target from a larger one a few cm closer (with a faint echo immediately following a relatively louder one), it is doubtful that variable refractory periods can fully explain echo resolution. It is interesting to note, therefore, that there is a mechanism obviously functioning that would be predicted to permit just such resolution. This is the phenomenon of spontaneous activity. We have long been familiar with the advantages of spontaneous activity in increasing sensitivity of a sensory system and in signaling both positive and negative changes in stimulus. Another less publicized advantage is the fact that some portion of the population is always refractory. In the case of primary auditory neurons, a large fraction fire at rates up to 100-200/sec. In a population of hundreds of thousands of cells, this assures that at any point along

the basilar membrane there will always be a significant number of sensory elements that are highly sensitive to vibration or receptor potential, others that are partially refractory, firing only too loud stimuli, and still others that are absolutely refractory and potentially free to respond to a later fainter sound. With considerable redundancy, synchrony of input from such cells can theoretically transmit reliable information at intervals down to the mechanical resolution of the basilar membrane. The same phenomenon could maintain a like degree of resolution at the cochlear nucleus where most cells are likewise spontaneously active, although at this level there is the beginning of potential for more complicated interactions and analyses.

Thus by invoking variable recovery rates, spontaneous activity, and grossly undetectable activity in the auditory nerve, it is possible to largely explain the bats' ability to hear and analyze most of the echoes returning even under adverse conditions immediately after each outgoing pulse. Not a totally satisfactory explanation, perhaps, but consistent, I think, with experimental data where such exists.

Some considerations with respect to "non-FM" bats.

Clearly, this explanation can apply only to animals emitting fast-sweeping FM pulses, extremely brief constant wavelength (CW) pulses, or clicks. Special problems face those employing long, predominantly CW signals. Perhaps they employ beamed outputs and directional hearing to eliminate most of the possible echoes; or it may be that the FM portion of such CW pulses, invariably found to

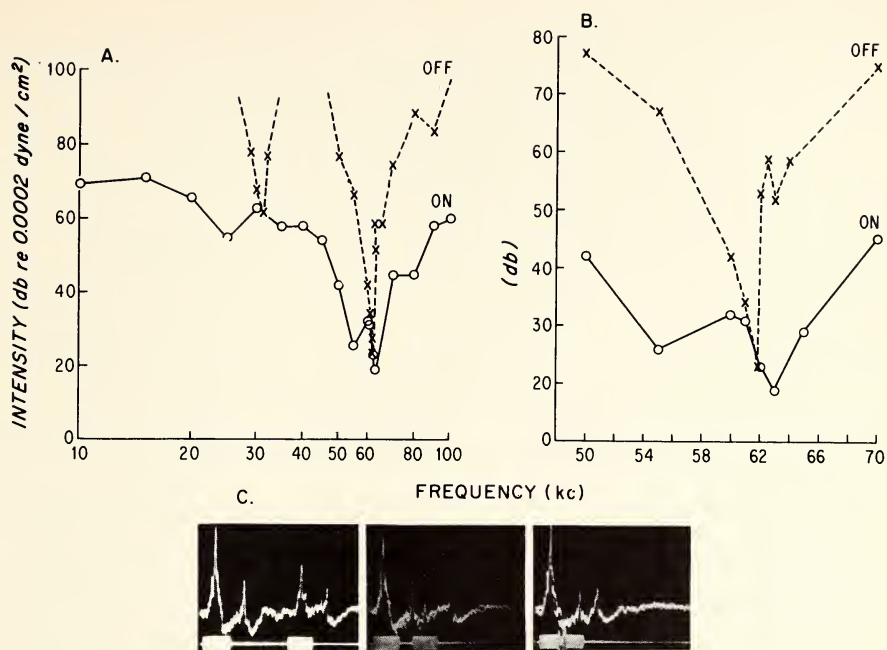


Fig. 4. A. Characteristic audiogram of Chilonycteris rubiginosa, made with the collicular positive evoked potential, showing the moderate tuning of the on-response and the much narrower tuning of the off-response.

B. A more detailed audiogram in the frequency range 50-70 kHz, showing the slight difference in "best" frequencies of the on and off-responses. Note the 27 dB drop-off of sensitivity of the off-response between 61.9 and 62 kHz. This drop-off was reversible and repeatable.

C. Records showing N_4 on and off-responses to pairs of 10 msec pulses at different intervals. The first stimulus was 60 dB above threshold, the second 40 dB above threshold. Note that as the two pulses are brought together to overlap the second on-response is lost, but the second off-response remains, as does the first off-response. The two signals were presented through separate loudspeakers.

some degree at the end of each pulse, is sufficient for the necessary echo resolution. Rhinolophus would seem the most interesting animal for study of this problem, but in the absence of any evidence regarding their neural analysis of echoes it may prove useful to report some preliminary findings with the neotropical bat, Chilonycteris rubiginosa. This bat emits a nearly CW fundamental (ca. 32 kHz) with one prominent harmonic (ca. 64 kHz) in a pulse lasting 15-25 msec and terminated by a brief (1-2 msec) downward sweep in frequency from approximately 32 to 28 kHz, 64 to 56 kHz (Novick and Vaisnys, 1964). Neurophysiological studies similar to those done with Myotis and Plecotus were made during a recent trip to Panama, with two relevant findings: (1) the evoked potential response (a reflection of single unit activity, also studied) is clearly tuned to the region of the bats' second harmonic, and (2) there is a prominent "off-response" that is even more narrowly tuned to a frequency just below the maximal excitatory frequency as well as to a second frequency, in the range of the bats' fundamental. Fig. 4a shows threshold curves for these responses in a typical experiment, with the frequency range between 50-70 kHz pictured in detail in Fig. 4b.

The narrowness of the sensitive band-width is probably a reflection of the bats' normal dependence on these frequencies alone, and undoubtedly represents a good method of eliminating interference by sounds outside these frequency ranges. The "off" response is particularly interesting, being a rare phenomenon in the auditory system, and rigorous controls were used to assure that it was not artifactual. This "off-response" was often as large and as sensitive as the "on" response at durations greater than one msec, and in some

cases was present down to 0.3 msec pulse duration. In contrast, recovery of responsiveness to the onset of a second tone pip was significantly slower than in Myotis or Plecotus, often being only 20-50% complete in 2 msec at N_4 . With long tone pips, more like the bats' own pulses, the potential value of this "off-response" became apparent, for faint second sounds, overlapping during most of their duration with preceding, louder sounds, could elicit clear "off" potentials, while the onset of the second stimulus was completely masked. The response to the "off" of the earlier, louder pulse was also prominent. Fig. 4c shows such a record. The use of an "off-response," either to record the end of the CW phase of a pulse or to analyze the downward sweep at the termination of each pulse, could provide an excellent means both of echo recognition and separate analysis of many overlapping echoes. For overlapping CW pulses it has the notable advantage that the nonoverlapping part of the echo is used, during which the background is likely to be fainter or silent.

Anesthetized Chilonycteris show a prominent response to the termination of natural orientation sounds emitted by other Chilonycteris. What fraction of this response is "off response," and what fraction is "on response" to the lower frequencies of the FM portion of the cry is not clear.

Overcoming ambient noise.

The remaining sources of interference that must be considered are those arising from the outgoing pulses of other bats and the variety of ambient noises present. It is important that a bat not

be confused at hearing bat cries it didn't itself emit and that it not be jammed by the noise of ultrasonic insects or rushing water or wind near it. On the other hand, under normal circumstances, many of these sounds are potentially informative: showing the location of potential prey or successful hunting companions, announcing the presence of obstacles, etc. All such sounds are presumably treated in the same fashion as meaningful echoes at the cochlea and in the auditory nerve, but can be recognized as meaningful or not to echolocation at some higher level that has been selectively encoded with and sensitized to the characteristics of the emitted pulse. In some cases, on the other hand, it is probable that the ambient noise can become so loud that echoes are in danger of being masked, in which case mechanisms of jamming resistance must be devised even at the most peripheral levels.

These mechanisms exist and have been studied in the context of laboratory attempts, mentioned earlier, to "jam" bats, especially the long-eared bat, Plecotus, with loud white noise. In these experiments, which have been described in detail elsewhere (Griffin, McCue, and Grinnell, 1963), bats were induced to fly from one end of a flight space to the other through an array of fine wires while noise covering their range of emitted frequencies was being broadcast at high intensity from 26 loudspeakers at each end of the space. The threshold of detection was finally reached when the total calculated energy in the echo of the measured outgoing pulse was on the order of -5 dB with respect to the power per cycle bandwidth of the ambient noise at the point of detection (i.e., the ratio E/N_0 was -5 dB). The theoretical

minimum for this ratio is between plus 1 and 10 dB, depending on the allowable false alarm rate.

At least a partial explanation for this spectacular skill, as deduced from electrophysiological studies, has also been described (Grinnell, 1963d; Griffin, McCue, and Grinnell, 1963). The most important factor seems to be the directionality of sensitivity resulting from the shape and orientation of the external ears, which are extremely large and complex in most bats. It has been found in Myotis and Plecotus that although the pinnae do serve as sound "collectors", the principal effect of the external ears seems to be a reduction in sensitivity at angles removed from the direction of greatest stimulating effectiveness. In both the horizontal and vertical planes, movement of a high frequency signal source may change the stimulating effectiveness by 2-3 dB per degree change in direction (Grinnell and Grinnell, 1965). If the bat can find an angle at which an important echo source is at the optimal direction, with interference coming from a less favored angle, especially on the other side of the head, then there can be as much as a 10-30 dB relative exclusion of the "noise". This was possible in the noise field used to jam Plecotus, and probably can explain their ability to resist jamming, since they appeared to take advantage of it. In addition to increasing the loudness of their outgoing cries and flying more slowly, they resorted to flying in zig-zags across the flight space, approaching a given wire almost head-on, but with the main source of noise at an oblique angle. The resulting 10-30 dB reduction in noise effectiveness is quite sufficient to explain signal detection by one ear.

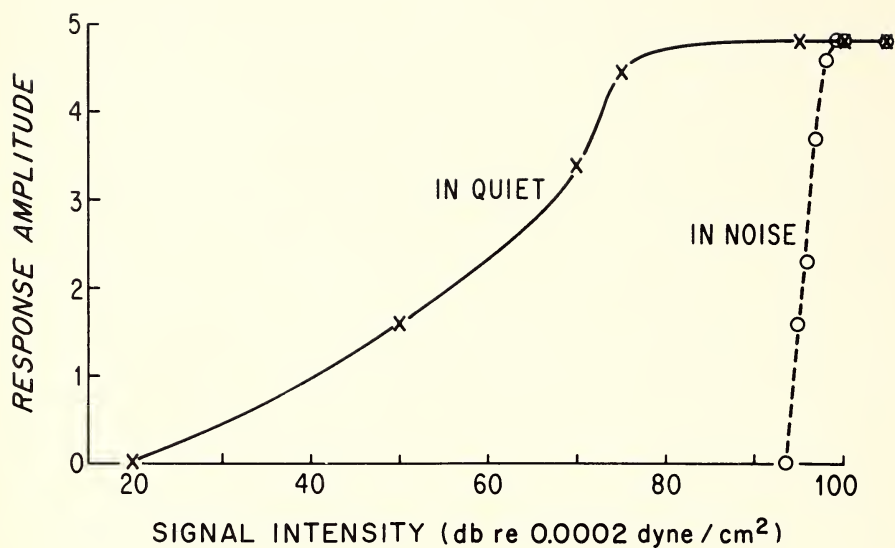


Fig. 5. Response curves made with the N_4 of Myotis, showing the normal relationship between signal intensity and response amplitude in the quiet, and the observed relationship when the signal was given in the presence of approximately 100 dB thermal noise. Signal frequency, 50 kHz.

In most such cases, however, the other ear will have been oriented in such a way that the noise arrived from a more effective angle than the echo, and yet detection by both ears is necessary for accurate localization of the target in space. Compensating for this problem is a type of binaural interaction wherein the presence of a detectable signal in one ear appears to reduce the effect of noise in the other by as much as 10-15 dB, permitting better discrimination than predicted in the colliculus receiving input predominantly from the ear most affected by the noise (Grinnell, 1963d; Griffin, McCue and Grinnell, 1963).

The capability of the auditory system to select or "amplify" the response to a meaningful signal in the presence of noise is seen in a variety of other ways. Often the threshold to a signal in noise was found to be several dB lower if approached from above rather than below threshold. Single cells were found that helped explain this behavior, varying by as much as 20 dB in "masked threshold," depending on whether the signal (at a repetition rate of 5-10/sec) was increased in noise to reach threshold, or noise was increased in intensity to mask a response (Grinnell, 1963d). In some cases, a remarkable degree of recruitment was seen in the growth of amplitude of evoked potential response to a signal as it rose above threshold in the noise. Full response amplitude could be reached within 5-10 dB of threshold, where in the quiet the same growth to the same amplitude required a 40-60 dB increase in stimulus. An example is shown in Fig. 5. This phenomenon may be analogous to the recruitment of populations in the response to faint second stimuli, as a response passes centrally.

CONCLUSIONS

An abundance of mechanisms exist to help explain bats' resistance to interference. Perhaps most important is the temporal precision which apparently enables them to independently analyze sounds arriving within 0.1-0.2 msec of each other. This may not represent an adaptation peculiar to the nervous systems of echolocating animals. Instead it is probably an expected consequence of a cochlea designed to accurately analyze frequencies as high as 50-100 kHz. The human cochlea, while designed to operate in a lower frequency range, is probably just as good an analyzer in this range. Nor is spontaneous activity, a postulated factor in the bats' (or even moreso in the dolphins') response at shortest intervals, a phenomenon restricted to echolocating animals. It seems likely that in humans or any other mammals there may be present in the auditory nerve a comparable amount of information about sounds arriving at an interval just resolvable by the basilar membrane, even though this interval must perforce be longer than in bats. At this point, however, there does seem to be a neural adaptation that is perhaps peculiar to echolocating animals. This is the central enhancement of recovery; the recruitment of larger and larger populations of units in progressively more central nuclei to deal with "second-stimulus" information carried by a very few auditory nerve fibers, even a number too small to be detected grossly in some cases. Human beings, and perhaps most other non-echolocating animals, appear instead to be organized in such a way that response to echoes or reverberations is actively inhibited.

The recruitment of response to "echoes" in bats is a result of short-term, frequency specific facilitation of large populations of auditory neurons. This facilitation probably is specific also for pattern of frequency change and signal duration, giving the bat auditory system another great advantage in signal detection: that of knowing the characteristics of the signal it is trying to detect. Such "coding" and temporal precision can at least partially explain a bat's ability to recognize and obtain information from its own echoes in the presence of tens of hundreds of other bats.

Also of assistance under these conditions is the sharp directionality of hearing observed in bats. Because of the high frequencies used, and the enlarged external ears, sound coming from most angles other than those most favorable for the ear are much reduced in effectiveness, and hence can offer much less interference. This appears to be the principal mechanism effective in helping bats resist "jamming" in laboratory tests with loud thermal noise.

It would be interesting to learn whether directionality of hearing is equally great in echolocating birds and cetaceans, where external ears are lacking. It has been shown (Payne, 1961; Schwartzkopff, 1962) that owls have considerable directionality of sensitivity even at frequencies below 15 kHz, and fine features of feather structure may be as effective as mammalian pinnae in creating such patterns. Also, there are now good indications that dolphins may attain directionality of hearing without external ears by coupling the cochlea to lower jaw or other head structures, resulting in sensitivity specific to certain directions (Norris, 1963; Yanagisawa et al., 1966).

In some bats, such as Rhinolophus, and perhaps in other echolocating animals, narrow beaming of the emitted pulse is probably also of great help in reducing interference by restricting the number of echoes that must be resolved and analyzed, albeit at the expense of losing information about targets or obstacles at angles out of the beam.

Finally, there appear to be binaural mechanisms that can selectively enhance the response to a signal in noise throughout the auditory system if it is clearly detectable in any one part. A good example of this is the reduced masking effect of noise in one colliculus when the signal is clearly detectable in the other. Noise has its expected masking effect at the level of the auditory nerve, but central to that, the auditory system somehow comes to respond selectively to the signal that had been largely masked in its input. The mechanism of this binaural interaction is unknown, and it is not even clear that the response to the signal is a response to information coming in through the "masked" channel. Perhaps it is rather a spread of response from the other channel: a recruitment of both colliculi to analyze signals that are normally sent predominantly only to one. If so, localization should still be hampered. Yet the bats do avoid obstacles under these conditions.

Obviously more questions remain than have been answered. Nevertheless, the evidence assembled does provide some hint of an eventual understanding of how bats and other echolocating animals manage to overcome the many forms of interference they face.

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ABSTRACT

Echolocating animals must hear and analyze echoes in the presence of the immediately preceding emitted pulse, other returning echoes, the cries and echoes of nearby companions, and ambient ultrasonic noise. Possible neural mechanisms for overcoming such interference are discussed with particular reference to bats. Two major factors are: (1) the neural discriminatory apparatus necessary for echo recognition, and (2) separate echo analysis down to intervals of 0.1 - 0.3 msec. Echo recognition results from the presence of large populations of cells whose firing patterns depend critically on signal parameters, and which are transiently facilitated to sounds having the same characteristics as one just heard. Temporal resolution depends on the high resolving power of the basilar membrane, on variable and often brief refractory periods of responding neurons, and perhaps on the small number of spontaneously firing units that are sensitive at a given time because they were refractory during a preceding sound. Directionality of sound emission and hearing can reduce interference from non-critical angles, while binaural interaction and recruitment of responses at ascending neural levels helps increase directionality and response to barely detectable signals.

DISCUSSION

par

H. MERMOZ

1- C'est en profane, mais avec le plus vif intérêt que j'ai lu d'abord, puis entendu, la conférence du Dr. GRINNEL.

Je ne saurais, bien entendu, me permettre le moindre jugement sur le contenu purement biologique de son étude.

Ce qui passionne le physicien, c'est évidemment de savoir si les Sonars Biologiques fonctionnent sur les mêmes principes que les Sonars imaginés par l'homme, pour ses besoins. Je me bornerai donc à lancer quelques têtes de pont entre Sonars Biologiques et Sonars Artificiels, du point de vue de la discrimination des signaux.

2- A juste titre, le Dr. GRINNEL, fait état de la gêne que constitue, pour la détection des échos, l'émission elle-même, pendant sa durée et quelques instants après. En fait, d'autres conférenciers ont précédemment contesté la notion même de gêne, et plaidé, au contraire, pour une interférence utile entre le début d'un écho et la fin de l'émission. La question n'est donc pas absolument claire, même entre biologistes. Le point de vue du Dr. GRINNEL coïncide avec celui des spécialités des Sonars Artificiels pour qui la gêne est incontestable.

Il existe plusieurs moyens de la réduire mais, en fait, les Sonars restent pratiquement sourds, pendant l'émission et pendant une fraction de seconde consécutive. Cette fraction est variable, mais dépasse en général largement les 100 microsecondes qui paraissent suffire aux chauves-souris pour récupérer tous leurs moyens de résolution.

3- Un des points les plus attrayants de la conférence, est, à mon avis, la référence à une possibilité, et même une probabilité d'existence d'un mécanisme selon lequel le signal d'émission "s'imprimerait" pour une certaine durée, en raison de sa puissance même, dans une "mémoire". Cette mémoire conserverait ainsi, au niveau du système de réception, un "modèle" ou une "copie" des échos attendus, échos supposés, en première approximation, identiques au signal émis.

Cette terminologie est tout à fait évocatrice pour les spécialistes du Sonar et du Radar. Ceux-ci, en gros, distinguent en effet deux classes de procédés, pour extraire les signaux des "interférences" parasites.

- a) dans la première classe, on range les procédés "grossiers" qui tiennent compte seulement de l'augmentation de puissance globale, qui est due à l'écho, pendant le temps où celui-ci se superpose aux parasites sans tenir compte de la forme d'onde qui apporte ce supplément de puissance.
- b) dans la seconde classe on range des procédés plus subtils, qui tiennent compte précisément de cette forme en comparant l'information incidente à une "copie" du signal attendu. Cette comparaison s'opère de façon continue à travers un filtre (Filtre Adapté) dont le gain est une réplique du spectre du signal, (copie spectrale). On peut la faire aussi d'une façon équivalente, avec un corrélateur utilisant la copie temporelle du même signal.

Dans tous les cas, la tension de sortie est proportionnelle au "degré de ressemblance" (corrélation) de l'information reçue avec la copie, et, par conséquent, à la probabilité de la présence du signal dans cette information.

Il serait du plus haut intérêt de savoir à laquelle des deux classes appartient le sonar de la chauve-souris. Le second procédé est évidemment beaucoup plus puissant, et la théorie montre que dans certains cas (bruit à spectre uniforme et gaussien) il est optimal.

Il n'est pas possible de conclure de façon définitive, bien que le Dr. GRINNEL offre quelques présomptions en faveur de cette seconde classe : existence de cellules plus sensibles aux impulsions modulées en fréquence qu'aux impulsions "à fréquence pure" ; de telles cellules fonctionneraient donc, au moins partiellement, en Filtres Adaptés.

- Dans quelle mesure ?

- Et à quel niveau sensoriel ?

Telles sont les deux questions qui dérivent tout naturellement des commentaires précédents. Nous reviendrons sur la première.

Pour la seconde, sa réponse définirait le degré de spécialisation atteint par la chauve-souris par rapport à l'espèce humaine. Il paraît à peu près certain, en effet, que l'oreille humaine perçoit un signal modulé-dont elle n'a aucune raison génétique de posséder le modèle - fréquence par fréquence, et qu'elle le transmet sans modification au cerveau. C'est à ce niveau que s'opère, le cas échéant, la comparaison avec un "modèle" acquis par apprentissage. La chauve-souris aurait-elle réussi à transférer cette fonction de comparaison à l'oreille interne ? Elle aurait alors réussi à construire le récepteur aval du cerveau et à soulager celui-ci en ne lui transmettant que le résultat de la comparaison. Mais ceci n'est encore qu'une hypothèse.

4- L'utilisation du procédé de " Comparaison avec la copie" appliqué à des signaux F.M. peut expliquer la fantastique discrimination en temps (et par conséquent en distance) dont se révèlent capables les animaux étudiés.

En effet, ce procédé transforme un signal long (et de faible amplitude) en un signal bref (d'amplitude élevée).

Le rapport des amplitudes explique l'efficacité du procédé pour la détection des signaux faibles (car le bruit ne bénéficie pas du même "renforcement").

La compression en durée explique, à la limite de détection, le pouvoir de discrimination. En effet, deux échos superposés avant la compression peuvent se trouver séparés après. Cette compression en durée a toutefois une limite théorique donnée par l'inverse de la largeur de bande du signal. Donnons un exemple considéré comme plausible par les Drs. GRIFFIN et GRINNEL.

L'un des animaux étudiés module son signal entre 80 et 50 kHz. La durée de ce signal est environ 1 milliseconde. Un signal à fréquence pure de même durée ne permet pas - à la limite de détection, c'est-à-dire dans des conditions sévères où toute l'énergie du signal est nécessaire pour percevoir sa simple présence - une discrimination en temps inférieure à 1 ms (34 cm environ).

Dans les mêmes conditions l'impulsion modulée (largeur de bande 30 kHz) permet une résolution limite de 33 microsecondes, (soit 1 cm environ).

La différence d'ordre de grandeur est suffisante pour qu'on puisse espérer une réponse significative à la question-clé suivante :

Peut-on mettre en évidence chez ces chauves-souris un temps de discrimination inférieur à la durée de l'émission, et ceci dans des conditions suffisamment sévères, où la perception directe des "fronts raides" avant ou arrière de l'impulsion-écho n'est plus possible ?

Une réponse affirmative à cette question plaiderait très fortement en faveur du procédé de comparaison avec la copie. La valeur trouvée (entre 34 cm et 1 cm) serait une réponse à la question n° 1 du § 3. Une réponse négative montrerait peut être que c'est seulement "sur signaux forts" (c'est-à-dire sur les fronts raides des échos) que de bonnes discriminations sont possibles, ce qui peut être alors considéré comme "facile".

A vrai dire la chauve-souris peut avoir une autre raison, pour utiliser des signaux F.M. , que la discrimination en distance sur signaux faibles. En effet, la théorie montre qu'un tel signal, même traité par un procédé de la classe a) est supérieur au signal à fréquence pure de même durée lorsque le parasite dominant est la réverbération (ce qui doit être fréquemment le cas). Cette supériorité s'exprime alors en décibels par

$$5 \log BT$$

où B est la largeur de bande et T la durée (30 kHz et 1 ms dans l'exemple précédent. On a alors $5 \log BT = 7,4 \text{ dB}$).

Cependant le même gain passe à

$$10 \log BT \quad (14,8 \text{ dB})$$

avec un procédé de la classe b), qui implique évidemment un degré de complexité plus élevé du récepteur.

Les Sonars Artificiels posent déjà, à cet égard, des problèmes de compromis difficiles entre efficacité et complexité (et prix). L'homme aimerait fort, à cet égard, prendre conseil de la chauve-souris ou du dauphin !

Si des réponses significatives ne peuvent être données aux questions précédentes, il serait intéressant, du moins, de savoir si les chauves-souris "élargissent" la bande de leurs impulsions modulées en proportion des "difficultés de vol" qu'elles rencontrent.

5- Si certaines descriptions du Dr. GRINNEL semblent en faveur d'une "comparaison avec la copie" , d'autres suggèrent cependant des mécanismes de détection assez différents. C'est la cas par exemple, du type de cellule sensible illustré par la figure 1 de sa conférence. Cette cellule est caractérisée par une zone de réponse et une zone d'inhibition, zones elles-mêmes commandées par d'autres cellules. C'est en somme, un résonnateur dont l'accès est ouvert ou fermé par d'autres résonnateurs.

La cellule répond à sa fréquence f caractéristique sous condition :

- a) que cette fréquence existe dans l'information incidente,
- b) que cette présence n'aie pas été précédée par la présence d'autres fréquences considérées comme incompatibles avec f , en valeur ou en position, par rapport à une séquence-type de fréquences successives.

Il suffit alors de remplacer la fonction d'inhibition par la fonction complémentaire de déblocage pour imaginer un modèle de détecteur constitué par une cascade de résonnateurs se débloquent les uns les autres dans un ordre bien défini. Seule la séquence-type est en mesure par conséquent de se glisser au bout de la chaîne.

L'arrivée d'un signal au bout d'une chaîne (le fait même que le dernier résonnateur se débloque) est un test de la présence récente de la séquence-type dans l'information incidente.

Il n'est pas nécessaire, dans ce schéma, de concevoir des chaînes de cellules rigidement liées, mais seulement un étage de cellules pour la fréquence initiale f_1 de la séquence-type, un étage de cellules f_2 etc... f_n .

Comme dans les étages de sélection d'un central téléphonique chaque cellule f_1 peut accéder à plusieurs cellules f_2 et débloquer la première disponible à l'instant opportun. Il faut donc beaucoup de cellules f_1 puisque celles-ci sont susceptibles d'ouvrir le processus de détection toutes les fois que f_1 apparaît.

Mais il suffit de ~~peu~~ de cellules f_n puisque celles-ci ne sont atteintes que par les vrais signaux.

Il y aurait donc là un test possible de la validité de ce schema. La question qui se pose est la suivante : la séquence-type (le signal F.M.) de l'animal étant connu, existe-t-il une nette disproportion entre le nombre des cellules sensibles à la fréquence initiale et le nombre de cellules sensibles à la fréquence finale.

-6 - On pourrait bien avoir l'impression que les chauves-souris qui n'utilisent pas de signaux F.M., sont nettement défavorisées par rapport aux autres.

De fait, le Dr. GRINNEL se penche sur leur sort et suggère quelques mécanismes compensateurs susceptibles d'expliquer pourquoi ces animaux ne sont pas plus maladroits que les autres.

Comme on peut s'y attendre, leur audition bénéficie d'une selectivité plus étroite, adaptée à leur signaux "à fréquence pure", ce qui élimine, au moins une partie des bruits ambiants. Néanmoins, ils sembleraient mal équipés pour se défendre contre la réverbération

En fait, ils peuvent dans une certaine mesure, rattraper ce handicap par une selectivité spatiale plus efficace que celle des "chauves-souris F.M."

En effet, à bande très étroite il est plus facile de produire dans le diagramme de directivité d'une antenne, en modifiant légèrement sa structure, des "zeros" (disons: des valeurs très basses) dans une ou plusieurs directions également ajustables. Dans une ambiance reverberante il est bien rare d'avoir affaire à une repartition uniforme de sources "parasites" dans toutes les directions. Plus généralement il existe quelques directions de "gêne prédominante" d'où reviennent des échos qui brouillent la direction d'écoute privilégiée. Il est alors plus facile d'atténuer fortement ces directions à bande étroite qu'à bande large.

Il est intéressant de rapprocher de cette possibilité théorique, une remarque faite récemment par le Dr. MÔMRES, selon laquelle les chauves-souris de cette catégorie se singularisent, au cours du vol de chasse, par des mouvements d'oreilles plus marqués que dans les

autres espèces.

D'autre part le Dr. GRINNEL a insisté, plus dans sa conférence que dans son texte écrit, sur la possibilité d'une interaction entre les deux oreilles. Cette possibilité existe en effet dans les Radars et Sonars Artificiels, entre deux antennes ou deux portions d'antenne.

Dans une situation un peu idéale où :

- a) l'une des deux parties ne reçoit que du bruit.
- b) l'autre partie reçoit du signal et du bruit.
- c) les deux bruits sont assez fortement corrélés.

Il est intuitif (et calculable) qu'on peut réduire les deux bruits l'un par l'autre au profit du signal. (A la limite, avec deux bruits identiques, une soustraction l'annulerait).

Dans une situation un peu plus réaliste où les deux parties reçoivent du signal et du bruit mais dans des proportions différentes, il est encore possible de définir la combinaison optimale qui avantage le plus le signal.

Ces idées simples se rattachent au fond à la théorie de la meilleure utilisation de l'antenne totale .

Pour tester si les chauves-souris appliquent réellement de tels principes on peut imaginer une expérience.

Celle-ci consisterait à les "brouiller" avec deux hauts-parleurs assez éloignés l'un de l'autre et équidistants du point de test.

Dans une première phase on émettrait le même bruit avec les deux hauts-parleurs. Dans une seconde phase on émettrait deux bruits de même intensité mais indépendants.

Si les chauves-souris connaissent à fond la théorie, elles doivent être nettement plus à l'aise dans la première situation que dans la seconde. Dans le cas contraire on doit constater une différence négligeable sinon un résultat inverse.

7- Les exposés de cette réunion constituent une leçon de souplesse

et d'adaptativité donnée par les Sonars Biologiques à nos Sonars Artificiels déjà bien complexes et encore bien rigides pourtant.

Que le Dr. GRINNEL me pardonne des suggestions peut-être utopiques et qu'il me permette d'exprimer à travers lui, mon admiration sans réserve pour tous ceux dont la patience et la minutie interrogent inlassablement les inextricables phénomènes de la Vie.

DISCUSSION

by

A. D. GRINNELL

Several people, foremost among them Dr. Mermoz, have raised the question whether bats may be using a matched filter or correlation network analogous to that used in chirp-radar, i.e., one that would have the effect of concentrating the output of the receiver in time, introducing a delay inversely related to frequency. This is impossible to answer, but I can make a few comments that I hope are relevant. The cochlea appears to work in just the opposite way than would be necessary for physical pulse compression. Highest frequencies are analyzed first, lowest frequencies last, and the neural response follows "analysis" at about the same latency in each case. It would be quite possible, on the other hand, that sensory nerves from all parts of the basilar membrane, representing all frequencies, might converge on a single analyzing cell (or population), and that the synapses could be of varying effectiveness to accomplish the same compression. Certainly the whole system doesn't work this way. Second and third order units are more narrowly restricted in frequency-response range than first order ones, nor has any

population of cells been found that does behave this way; but we cannot eliminate the possibility that a small side channel exists to do this.

On the other hand, I don't see any necessity for it. Given accurate frequency discrimination, which we know exists, it seems fully adequate to have each narrowly tuned population respond to a given frequency in the echo, having been temporarily facilitated by the same frequencies in the emitted cry. A moment later a different population is responding to a different frequency band, analyzing it for the information it contains. In a fast-sweeping FM pulse, the effective bandwidth will be extremely brief and exactly timed. Moreover, if I am not mistaken, pulse compression offers no improvement in signal to noise ratio, anyway. The noise over the whole bandwidth is compressed in the same way as the signal. As long as the cochlea can simultaneously analyze different frequencies occurring in different returning echoes and, if necessary, in the emitted pulse, I see no advantage in matched filters or pulse compression.

Another question concerned the downward sweep of the FM pulse. Why does it seem invariably to be downward? I don't fully understand Dr. Mermoz's thought that this would eliminate Doppler ambiguity; but we came up with two or three possible reasons in discussion the other day, the simplest of which is that it might be impossible, physiologically, to produce upward sweeping pulses of the equivalent intensity, brevity, and frequency bandwidth. I would like to add one more possible reason that hasn't yet been voiced. This is a result of the way the cochlea functions. High frequencies are analyzed near the basal end, lower frequencies further in, and the traveling wave on the basilar membrane is damped out quickly beyond the point appropriate for analyzing the lowest frequency component in a given sound. If the pulses were sweeping upward, the low frequency energy would partially excite all the basilar membrane receptors enroute

to the low frequency end, and these would be progressively more and more masked as the pulse swept upward to high frequencies. On the other hand, a downward sweeping pulse permits analysis of each successive frequency on relatively unexcited membrane.

The question of "quality factor" has been raised several times, and I'm afraid some people may have misunderstood my assertion that signals 100 microseconds apart can probably be heard and analyzed independently. I don't suggest that single cells can do this. Probably the minimum necessary recovery time for auditory cells is 0.5-0.6 msec, and this limit is set, not by the damping of the system, but by the time constants of permeability changes in the cell membrane due to synaptic or spike activity. Similarly, the high degree of tuning of higher order auditory cells is not a function of their damping or resonance. The increased sharpness of response is a result of neural inhibition. The only necessary component for which a Q-value in the normal sense might be applicable is the basilar membrane. It must be sufficiently damped to permit distinguishable peaks of deflection at intervals of 100 microseconds or less. This would require a bandwidth of 10 kHz or more--quite in keeping with the response curves of first order neurons. Within this 10 kHz range, however, units may be more or less strongly excited, permitting later neural interaction to sharpen the tuning of response.

The role of the pinna in echolocation has been queried on several occasions, especially in Rinolophus, where the ears move in synchrony with outgoing pulses. I feel it is likely that the resulting warble in Doppler shift of echoes might provide important information both for detection and relative velocity calculation. Perhaps even more important, however, is the possibility that this rapid ear movement, in opposite directions in the two ears, might be used to determine the vertical angle of target

sources, by a comparison of intensity at the two ears. As you know, I have my own pet theory about how FM pulsing (or for that matter, all) bats might localize targets in three dimensional space, i.e., by the binaural comparison of intensities at 3 or more different frequencies. (Grinnell & Grinnell, 1965). Measurements of the effects of the pinna on directionality of sensitivity show that although they do slightly increase sensitivity in certain directions their principal function is rather that of reducing sensitivity from other directions: contralateral to and below the animal, especially. Thus they help create highly directional receiving patterns that are made sharper still by binaural interaction. In the bats so studied, such binaural intensity comparison could, I think, explain target localization in both the X and Y planes. Time differences are probably not usable, since the interaural distance is so small. The same consideration applies to the simultaneous binaural frequency difference from an FM pulse returning from one side. This binaural difference would have to be analyzed two or three synapses deep in the system, where it would be identical to a time difference at any given frequency. A final thought about large pinnae: One finds them often in the "whispering" bats. These large pinnae are particularly effective in "collecting" echo energy, and probably also in excluding emitted pulse energy. The resulting enhancement of echo reception, coupled with the relatively large amplitude of echoes returned from close objects at short intervals when the bat is hovering, both help explain the faint output used by such whisperers.

Two discussants have raised the question of "jamming" by moths---the ones shown by Dunning and Roeder to respond to pulses of ultrasound by emitting pulses of their own, which appear to deter attacking bats. I feel, as did those authors, that the mechanism is very unlikely to be true

jamming. It seems much more likely that these moth sounds are active advertising, the equivalent of warning coloration, announcing "Here I am---but I taste awful and have long spiny legs". Even if this isn't true, they might be imitating moths that are distasteful for these reasons.

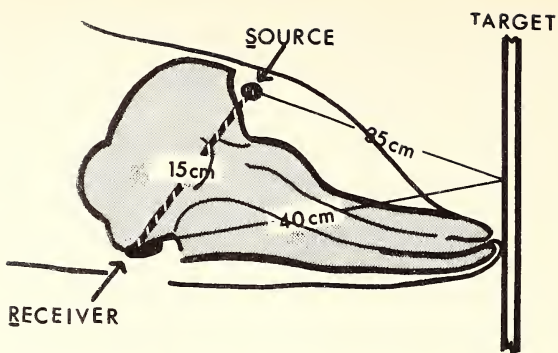
Finally, as in previous discussions, I feel that I should rise to the defense of bats, to stand behind the assertion that they can do more than merely resolve targets. I feel that they can accurately determine distance. All of the evidence I can cite is indirect, but some of it seems to me to be convincing. Much of it comes from the work of Fred Webster, who will, I hope, correct any of my errors. The avoidance of wires seems to me to indicate distance determination. Bats almost certainly detect large objects well before they increase their repetition rate, which they apparently do immediately on detecting a much smaller object near them. Such small targets cause them to dodge sharply, immediately after detection, while larger ones are avoided very gradually, with no abrupt maneuvers. During landing, they approach to within about 10 cm of a crack in the wall, then flip over and land with their hind claws approximately on the crack. In drinking, they know just where to level off (in a smooth flight path) to dip in lower jaw and tongue, no more. In insect capture they appear in some cases to be able to extrapolate a target's direction and speed of movement and fly in the optimal direction to intercept it. They know just where to reach with a wing-tip to capture an insect, even when the last usable information (because of reaction time) must have come several cm away; and they can flawlessly capture insects that are close to other obstacles, such as tree branches or the ground. The neural apparatus for distance determination surely exists. If they can't determine distance, they are extremely lucky.

DISCUSSION
by
William E. EVANS

I will not comment directly on the content of Dr. Grinnell's comprehensive and lucid discussion of the mechanisms for overcoming interference in echolocating animals. I would, however, like to offer a few additional comments on some of the problems discussed, especially in regard to echolocation in the aquatic environment.

Interference From Emitted Pulses:

Interference from the outgoing pulse is most likely an important source of interference to echolocation in aquatic mammals e.g. delphinids. However, this problem may be no greater for echolocating aquatic mammals than it is for the bats. Although the speed of sound in water is about five times greater than that in air (34.4 cm/msec. in air, and 150.0 cm/msec in water), the size of all known aquatic echolocators is much greater than that of any species of bat. Therefore, the inter-aural distance and the distance from the source to the ear of the producer are also considerably greater. As an example, the distance from the proposed echolocation pulse source in an adult Atlantic bottlenose dolphin (Tursiops truncatus) to the tip of the rostrum is approximately 35 cm (2,5). The distance from the tip of the rostrum to the ear is about 40 cm. The total distance traveled by an emitted pulse from the source to a target at the



$$\begin{aligned} S \rightarrow T \rightarrow R &= 0.5 \text{ msec} \\ S - R &= 0.1 \text{ msec} \end{aligned}$$

Fig. 1. - A composite diagram showing possible distances of sound paths through the head of a dolphin from the source to the ear and from the source to the tip of rostrum. Distances used represent the mean of measurements made on the skulls of three adult Tursiops truncatus.

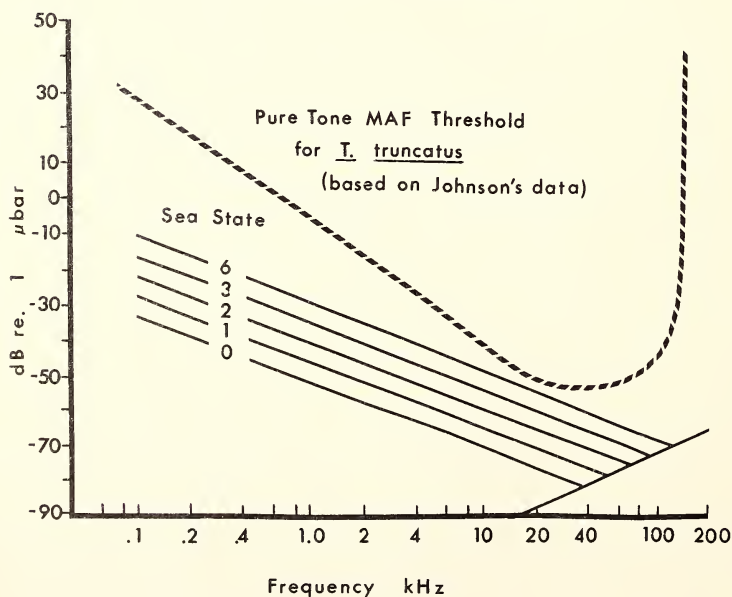


Fig. 2. - Pure tone auditory threshold curve of an Atlantic bottlenose dolphin, Tursiops truncatus (4) compared to open ocean ambient noise measured at various sea states (7).

end of the rostrum and the echo return to the ear is 75 cm or an elapse time of about 0.5 milliseconds. If it is assumed that sound travels at about the same velocity in tissue as it does in water, there would be about a 0.1 msec delay in the animal hearing (distance of 15 cm) its outgoing pulse. Thus with the animal's rostrum touching a target, the time difference between the emitted pulse and heard echo would be a minimum of 0.4 msec (Fig. 1) for an adult Tursiops. In addition the duration of echolocation pulses for some delphinids (Tursiops and Steno) vary from less than 0.1 msec to 0.5 msec with an average value of about 0.2 msec. Although larger values than these (1.0 - 2.0 msec) have been given (2), most of these longer pulse durations are based on measurements made on limited bandwidth equipment (100 hz - 15 kHz) with the animals in highly reverberant enclosures. In either case, delphind pulses are generally shorter than those used by bats.

Considering the length of pulse and the built-in minimum temporal separation of emitted pulse to echo, there would be no overlap of the outgoing pulse and the echo even at the observed maximum repetition rates of 500 (Evans, Johnson this volume). If one wished to speculate that echolocating aquatic mammals i.e. delphinids,

have neurophysiological mechanisms similar in function to those Dr. Grinnell has demonstrated for bats it would appear then that the problem of interference from the outgoing pulse should be no greater for aquatic echolocating mammals than it is for their aerial counterpart, the bat.

Target Recognition:

If we look at the problem of discriminating echo returns from a wide variety of objects as essentially non-echolocating mammals, it appears indeed formidable. However, with the neurophysiological capability demonstrated and described by Dr. Grinnell this may not be an overwhelming problem for an echolocating animal, especially in the context of his natural environment. Different food targets most likely vary considerably in size, material composition, pattern and speed of locomotion. Learning undoubtedly plays an important role in this aspect. Where several aspects of a target are needed for full recognition, the target may need to not only produce an echo like a food object (insect, fish), but move like an insect, be within the appropriate size range, and be in the proper environment. Some of these factors are undoubtedly more important than others. Generally in the initial training stages it is not easy to get the dolphin to take "dead" food. Once a particular type of food is taken a certain amount of time is needed to change to a different size and type of food fish.

We should also consider the factor of attention in the matter of resistance to jamming. Just as man can attend successfully to one conversation or one voice in a group of many voices or attend to one musical instrument in a quartet of musical instruments, the animal, dolphin or bat, most probably can attend to an echo of importance in a complicated ensemble of echos. Attention may also be of some import in the identification of an echo associated with a specific pulse. Each echo will bear a correlated and somewhat predetermined relationship in time and direction with the outgoing pulse which it represents. Combinations of these factors should provide target signatures that fall well within the discrimination limits demonstrated neurophysiologically for bats and behaviorally for delphinids (Norris et al, and Evans and Powell, this volume)¹. One would suspect that this would hold equally true for static targets such as trees, branches, buildings and their underwater counterparts.

Ambient Noise:

Delphinids are faced with essentially the same types of interference from ambient noise as those elaborated by Grinnell for bats. In delphinids, however, the problem may be more pronounced, particularly in reference to the

¹Some of the acoustical parameters of targets and their effects on the echo signature are discussed in detail by Johnson, this volume and by Norris et al.

emitted pulses of companions. This is especially true in light of Basitan's work (this volume) which indicates that some of the pulse output of Tursiops may be communicative as well as echolocative.

As is the case in bats, delphinids probably avoid much of the ambient noise problem by the use of ultrasound since most of the acoustic energy in the sea ambient is below 10 kHz (7) and the most sensitive range of hearing is from 10 kHz to 100 kHz (4) (Fig 2). In addition to this, Dudok Van Heel (1) has demonstrated a high degree of directionality of hearing in the common harbor porpoise, Phocaena phocaena. This well-developed sense of directional hearing, if it exists for other species, and the apparent narrow beaming of the emitted pulse (3, 6) could account in large part to the apparent success of delphinid echolocation even in extremely noisy environments. Dr. Grinnell expressed the opinion that the narrow beaming of the emitted pulse might be at the expense of losing information about targets or obstacles at angles out of the beam. This may not be the case, at least in Tursiops, since the head scanning which is associated with echolocation in most species observed, allows the animal to cover a very broad field directly ahead (50° right or left) with a beam as narrow as 10° . In addition, the width of the beam of outgoing dolphin's echolocation pulses appears to be frequency dependent (6). The echolocation pulses of most dolphins appears to have energy distributed over a broad-

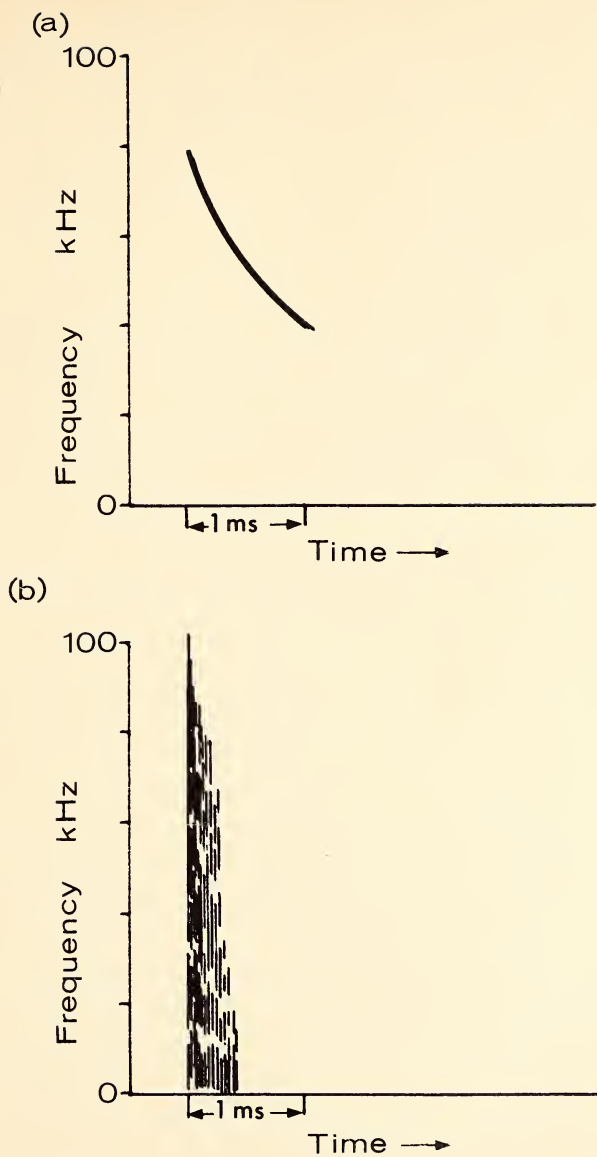


Fig. 3. - Spectrographs of a typical bat (Myotis species) and dolphin (Tursiops truncatus) echolocation pulse.

band of frequencies (200 Hz - 150 kHz). Energy below 40 kHz is distributed over a relatively wide beam narrowing progressively as the frequency increases.

In any discussion of the interference problems encountered by an echolocating animal it is necessary to be aware of the characteristic of the signal being used to gain echo information. This is especially true in any comparison of aerial echolocators to aquatic echolocators. As has been well established at this symposium bats use a relatively short, basically single frequency (range 20 kHz - 90 kHz), more often than not frequency modulated pulses. The few species of delphinids that have been adequately studied use a profoundly different type of pulse for echolocation. The pulse produced by Tursiops truncatus is very short in duration (0.2 - 0.7 msec), containing energy throughout a broad range of frequencies (20 - 150 kHz). Characteristic frequency - time patterns for a typical bat pulse, and a typical dolphin pulse are presented in Fig. 3 for comparisons. Although no quantitative studies have been made one would intuitively think that the resistance to interference i.e. jamming, of each of these two types of pulses would be significantly different.

In closing I would like to reemphasize Dr. Grinnell's statement that most of this material is speculative in nature. However, I would like to note that with the

neurophysiological and behavioral data available on the echolocation ability of bats and more recently delphinids, we now have a firm format within which a comprehensive understanding of biological sonar systems can be built.

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DISCUSSION

par

L. GERARDIN

Le schéma de recep-teur de chauve-souris étudié par l'auteur offre une similarité frappante avec les récepteurs de radar Pulse-Doppler les plus évolués en cours d'étude : batterie de fil-tres à accords décalés, logique de comparaisons et de seuils entre fil-tres, sans oublier l'action de duplexage émission réception de certains muscles et de seuils de neurones.

Les largeurs de bande des résonateurs : 2 à 5 kHz, sont parfaitement bien adaptées aux durées des signaux émis et à la modulation de fréquence qui y existe (chez les Vespertilionidés).

La mesure de fréquence par observation de 2 à 3 cycles est un peu à la limite de la constante de temps de ces fil-tres, il faudrait étudier ceci plus en détail. La surtension de 10 n'a rien d'extraordinaire (je n'ai vu mentionné nulle part dans la communication de données concluant à une surtension de 10 000 et à des bandes passantes de 3 cycles !).

L'emploi possible d'une analyse de structure interne d'un signal FM par une cascade de réponses de fil-tres successifs est fort intéressante. Elle pourrait expliquer la résistance au brouillage par bruit blanc et la non perception d'échos de grandes dimensions (arbre, etc.) qui ne renvoient pas en réalité un écho pur mais une sorte de bruit du fait de la totale décorrélation mutuelle des signaux renvoyés par les multiples points réfléchis-sants de la cible de grande dimension.

Mais est-il possible d'expliquer par ce processus l'in-sensibilité d'un animal au brouillage mutuel des signaux émis par ses congénères. Connait-on exactement la dispersion autour d'un signal type des signaux émis par des individus variés, et quelle serait la précision de l'analyse fréquentielle capable de sépa-

rer les signaux particuliers de deux individus différents ? Est-elle compatible avec des bandes de 2 à 5 kHz pour les résonateurs individuels ? On peut en douter.

La directivité des émetteurs (bouche) et des récepteurs (oreilles) est, comme le signale A.D. GRINNELL, un facteur probablement beaucoup plus efficace.

Dans ce domaine de la résistance aux signaux interférents, il est un autre point qui semble mériter quelques réflexions, c'est celui de la lutte moucheron-chauves-souris. Dans les études sur le sujet faites par le groupe de Tufts University, on voit décrits les récepteurs d'écoute des mouchérons (tout au moins de certaines espèces), leur comportement de fuite, puis d'évasives rapides si la chauve-souris continue à se rapprocher et finalement l'émission de brouillage par clics très brefs si le prédateur arrive au contact. Très généralement, l'émission de clics provoque chez la chauve-souris une réaction de rupture de la poursuite. Ceci a été confirmé par les mesures en laboratoire (en particulier Science, janvier 1965, p. 173-174). Deux hypothèses explicatives sont alors possibles : ou bien le brouillage agit comme un brouillage, en ce sens qu'il perturbe la poursuite, en particulier la poursuite angulaire. Ceci serait fort intéressant car l'analyse du phénomène devrait apporter quelques lueurs sur les processus de poursuite angulaire. Ou alors, il s'agit d'une simple indication de la part de l'insecte poursuivi : inutile de continuer la poursuite, je ne suis pas comestible. Dorothy C. DUNNING m'a signalé qu'effectivement la chauve-souris rejette en hâte un moucheron de ces familles brouilleuses si par inadvertance la poursuite s'est terminée par la capture. Cette seconde explication est très logique et ne pose pas de nouveaux points d'interrogation. Peut-on décider avec une bonne certitude quelle est, de ces deux hypothèses, celle à laquelle il convient de se rallier.

v

Actions réciproques
d'autres systèmes sensoriels
et du système sonar

Interaction
of other sensory systems
with the sonar system

INTERACTION OF OTHER SENSORY SYSTEMS WITH THE SONAR SYSTEM

by
G. NEUWEILER

Introduction

One of the vital tasks of every living creature consists of getting a maximum of detailed information on the nature of its environment in the shortest possible time. Animals obtain this information by sensate perception of different modality energy pattern emitted or reflected by extrinsic objects. The excitations produced in this manner are conducted to the brain where they are integrated into a complex excitatory pattern. Orientation in Vertebrates is possible only by virtue of transformation of spatial, extrinsic energy patterns into a spatially correlated excitation pattern within the central nervous system. The more energy modalities entering into the excitation pattern, the larger and the more detailed is the total amount of information. It is well known that the reticular formation of the midbrain, the thalamic nuclei, and the motor and association cortices contain regions where inputs of different sense organs converge. Recently MURATA and coworkers (29) succeeded in proving that in the visual cortex of the cat acoustic, somesthetic, and visual stimuli converge on a single neuron. Though cooperation of all sense modalities would provide maximum information, many animals rely on only a few of them. While not all energy modalities are equally well suited to representation of the environment, in some biotopes not all energy sources are available, or they disappear periodically. The ideal energy source would be an extrinsic, strong emitter with a constant or periodical energy flux. The stable gravitation field of the earth, and the electromagnetic radiation of the sun e.g. are

energy modalities favorable to orientation.

All Vertebrates determine their position in the 3 coordinates of the gravitation field of the earth predominantly by means of their equilibrium sense organs. Since these organs are invariable guides of all orientation actions, and since they do not reveal anything to the animal concerning the nature of its surroundings, further discussion will not be needed in this text.

The most suitable sense organ for environmental orientation is the eye. By a large spatially ordered point-to-point representation it instantly and simultaneously transforms patterns of sunlight reflexion from objects into a congruent excitation pattern on the retina. Since they live partly or mostly in darkness, echolocating vertebrates should have serious orientation problems: they use self-produced, variable sound pulses which yield only a temporary and spatially limited information about the more immediate neighbourhood. Whenever the sound production stops the flux of information will cease too. One might therefore suspect that such shortcomings are compensated for by means of other sensory systems.

So far no experimental investigations of the aspect of multi-sensory interaction have been carried out on echolocating terrestrial vertebrates. I will therefore try to gather a mosaic from various investigations on sense organs of the animals concerned, as well as from numerous occasional observations of students of echolocation.

Birds.

Collocalia or Cave-swiftlets of Southeast Asia are small birds which live in huge colonies and build their nests beneath the

ceiling in the darkest corners of natural caves. They roost during the night and fly out during the daytime to hunt insects on the wing. NOVICK (34) and Lord MEDWAY (25, 26) investigated the orientation of Collocalia brevirostris unicolor in Ceylon and C. maxima lowi in Malaya. Swiftlets entering a cave abruptly began to emit relatively low-pitched clicks at a rate of up to 6/sec. The rate increased as the birds approached their nests. Whenever a bird turned towards the light in the entrance it ceased to emit sound clicks. Captured Collocalia flew silently in a lighted room but started their orientation sounds the instant the electric light was switched off. Deafened birds were seriously desorientated. Even Collocalia that could hear normally clearly avoided to fly and usually roosted quickly. NOVICK found that cave-swiftlets living in fairly lighted caves never emit any clicks at all, and according to MEDWAY, C. esculenta lacks orientation sounds altogether.

Such observations disclose that Collocalia uses echolocation only when vision absolutely fails. During their hunting flights in full sunlight they most probably rely on vision as all other swiftlets not roosting in caves do also. Yet the use of echolocation in the pursuit of insects is still possible. The nature of their orientation sounds however, makes it highly improbable. From small objects the low-pitched pulses of 4-5 kHz/sec do not reflect as well as those of the bats, which are pitched ten times higher. Apart from that, the low repetition rate of up to 10/sec conveys only a small fraction of information/time unit if compared to the repetition rate of more than 100/sec in bats when close to their prey. Recently DÜCKER (10) described numerous

greenish to colorless oildroplets in the cones of the retina of C. esculenta. But she found only a small percentage of yellow and red ones. This predominance of greenish oildroplets is found again in owls and night-jars, but forms a marked difference to other diurnally active birds. There is no physiological data on the vision of cave-swiftlets available but the abundance of oildroplets and cones in the retina of Collocalia strongly suggests a good, if not excellent, vision. One is tempted to assume that in cave-swiftlets echolocation is of recent date only, and as yet, is in a poorly developed state. Such an opinion is supported by the following facts:

- 1) Echolocation appears only in Collocalia species living in dark caves.
- 2) Orientation sounds are low pitched.
- 3) The repetition rate of sound pulses is reversely correlated to light intensity. This forms a striking contrast to bats in which sound emission is independent of light intensity.
- 4) Cave-swiftlets are only diurnally active.

The last statement, however, does not apply to the South-American oil bird *Steatornis* studied by GRIFFIN (15): These birds roost during daytime in sections of caves which are completely dark. In the evening thousands of oilbirds fly out of a cave, producing a continuous noise of very sharp clicks of a mean sound frequency of 7,3 kHz/sec. The sounds are emitted in bursts of up to 6 clicks. Since GRIFFIN does not mention the rate of bursts during flight a clear figure of the repetition rate cannot be given. The oilbirds fly off to trees where they feed on fruit. As in the case of Collocalia, the oilbirds greatly diminish

their repetition rate while flying in light. Oilbirds with both ears plugged skillfully avoided all obstacles in a lighted room. GRIFFIN therefore concludes: "Evidently when light is available the oilbirds orient themselves by vision". To my knowledge nothing is known about possible sound production in oilbirds when flying in search of fruit in nocturnal dim light. The diminishing rate of clicks in light and the well developed eyes of Steatornis lead me to the assumption that vision plays an important, if not a major part, in nocturnal orientation as long as some faint light is available. Though echolocation is more intensive in Steatornis than in Cave-swiftlets, it again seems to be an adaptation to cave-roosting rather than an orientation mechanism during nocturnal activities. This view is supported by the results obtained by WINTER and SCHWARTZKOPFF (38). They show that Steatornis conforms to the general rule saying that in all birds, from the smallest singing bird up to the large eagle owl (only exception: night owls), the number of nerve cells in the hearing centres of the Medulla increases in proportion to the body weight 0,15.

Random noise hearing may also be an efficient aid, especially in locating enemies, but there is no data available on the physiology of hearing in Steatornis. In the case of the fruit-eating Steatornis smell may be an additional guide to food, but olfaction in birds is generally said to be poor.

Megachiroptera.

This is evidently not the case in another fruit-eating nocturnally active cave-dweller; the Flying Fox of the genus Rousettus. Among Flying Foxes this genus is the only one using

echolocation (28). During the daytime they roost in dark caves or vaults which they leave after sunset in search of sweet fruits. MÖHRES and KULZER (28) demonstrated that fast flying Rousettus can easily detect 50 mg banana of $0,005 \text{ cm}^3$ of banana ether by smell only. It is without doubt their fine sensitivity for odours that guides them towards the ripe fruit. Olfaction as well as extreme sensitivity to random noise are instruments for the locating of spots rather than for representation of the spatially fixed environment. For the latter purpose Rousettus relies on vision and possibly on echolocation.

GRIFFIN, NOVICK and KORNFIELD (18) showed that in complete darkness Rousettus can avoid wires down to 1,07 mm Ø and detect others of 0,46 mm Ø. Their tongue-produced orientation clicks contain a wide band of frequencies mounting up to 100 kHz/sec. The maximum intensity is confined to 12-18 kHz/sec. In a barrier experiment in complete darkness Rousettus aegyptiacus did not touch wires of 3 mm Ø 79 % of the time. But it invariably hit these wires as soon as intense thermal noise above 25 kHz/sec was played into the room. However, when the light was switched on, the Flying Fox instantly regained its former skillfulness. Even with continued noise it scored 90 % misses. This loss of orientation in darkness by ultrasonic noise as well as its immediate recovery in light indicates firstly that perception or neural processing of echoinformation are not yet as sophisticated as in insectivorous bats, and, secondly that vision yields as many, if not more, informative cues as long as some faint light is available. A Rousettus with ears plugged takes off without any difficulty and skillfully avoids all obstacles

Table 1. Thresholds of brightness - discrimination.

	D a r k - range	M i d d l e - range	W h i t e - range
Flying Fox	0/7	25/48	76/100
Hedgehog	0/3	22,6/46,5	73/100
Rat	-	29/50	-
Golden Hamster	1,1/2,7	31,2/46,1	68/100
Squirrel	0/2	30,7/41,5	74,4/100
Minnow	0/2,1	26,2/46,5	78,6/100
Man	2,1/4,3	22,6/17,9	78,6/100

Figures give the percentage of white - content in the signals at threshold level.

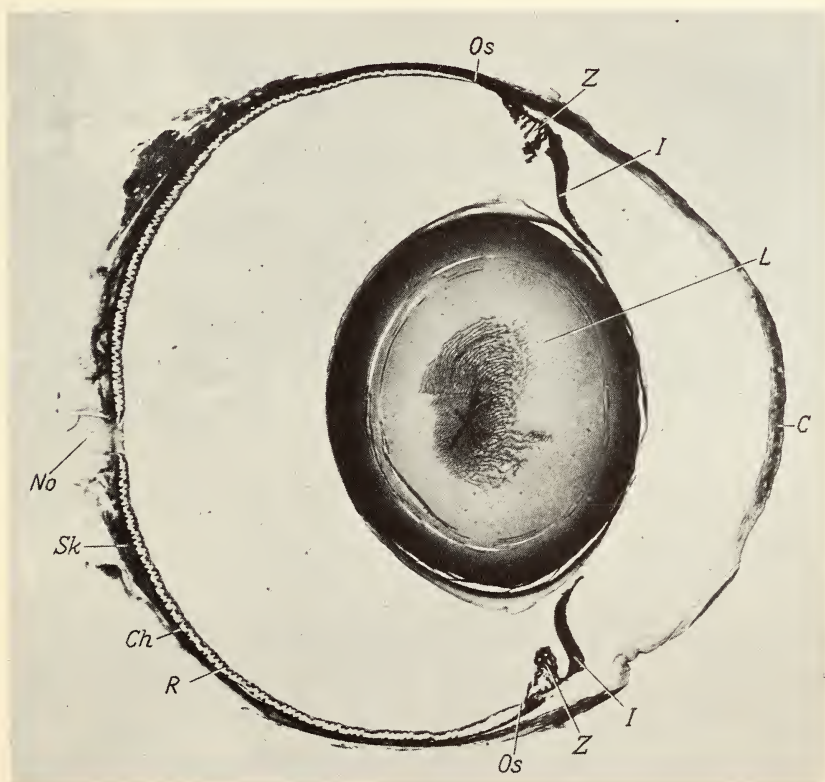


Fig.1. Meridian section through the eye of the Flying Fox *Pteropus gig. giganteus*. 8,5x enlarged.
C Cornea, Ch Chorioidea, I Iris, L lense, No optic Nerve, Os Ora serrata, R Retina, Sk "klera, Z ciliary body.

in a dimly lit room. As in the case of birds, the intensity and the rate of orientation sounds greatly diminish without ever ceasing altogether when Rousettus flies in daylight.

In 1962 I published a report on the structure and the function of the eye of Pteropus giganteus, the Indian Flying Fox (30). This close relative of Rousettus lives on trees in the open field and does not have any echolocation device at all (28), yet it searches for fruit under exactly the same conditions as Rousettus does. Except for darkness in caves, vision alone seems to make Pteropus as well orientated as the echolocating Rousettus during its nocturnal activities. A cross-section through the eye of Pteropus shows all features of a typical night-adapted eye (Fig. 1): The most eminent part of the eye is the large nearly spherical lens which occupies 60 % of the axial diameter. The cornea is more curved than the bulbus and covers 130° of the surface of the eyeball. Cornea and lens form a powerful refraction device yielding a refraction of 144 dioptre or a focal distance of only 9,23 mm compared to only 67 dioptre of 15 mm focal distance in the human eye. In spite of this great refraction, and due to the short lens-retina distance, the eye is far-sighted by + 2 dioptre only, as measured by skiascopic means. This extremely short-focussed refraction system produces a retinal image which is smaller but brighter than that of eyes of diurnal mammals. It also implies a wide depth of focus, so that an accommodation to objects at different distances may not be necessary at all. As a matter of fact the ciliary body is very narrow and contains no ciliary muscles. Experiments with pilocarpine and atropine proved that accommodation was missing. The

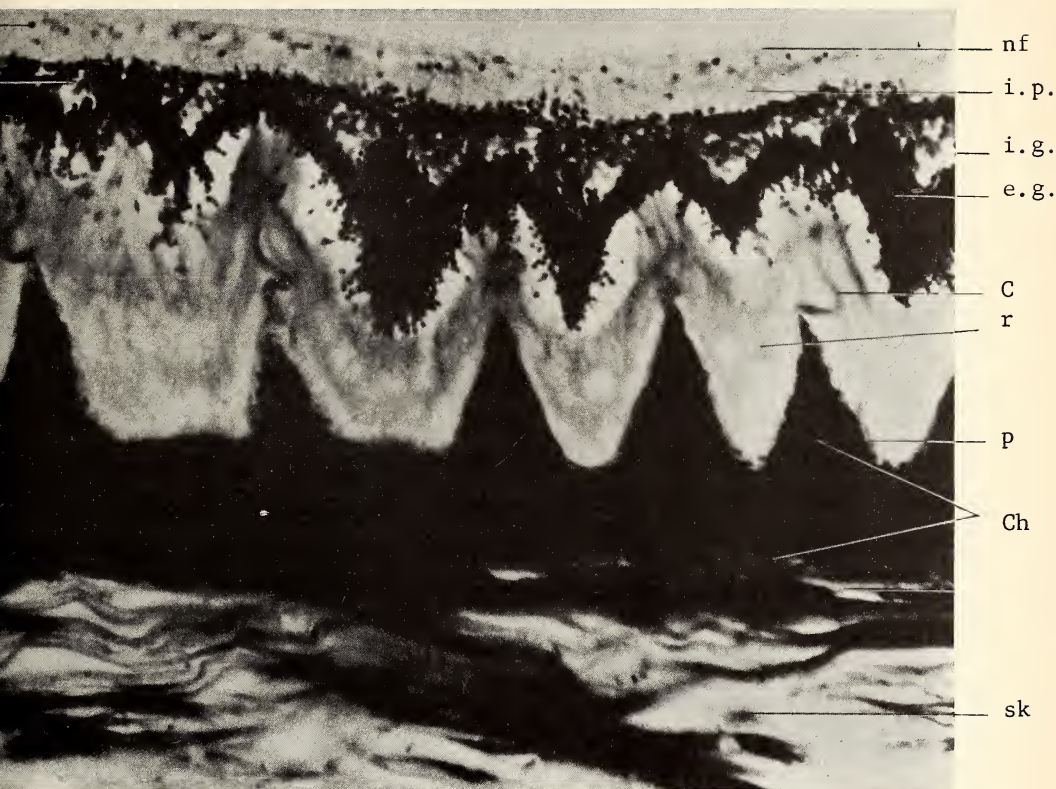


Fig.2. Sagital section through the retina of *Pteropus gig. giganteus*. 128x enlarged.

C capillary loop, Ch Chorioidea, e.g. external grain layer, i.g. internal grain layer, i.p. internal plexiform layer, nf nervefibers, p pigmental cell layer, r rods, sk Šklera.

visual cell layer contains only very thin, long, stretched rods. They are densely packed. 1 mm² contains on an average 672400 rods. This is one of the highest visual cell densities found in any mammalian retina. The ganglion cell layer on the contrary contains only 1585 ganglion cells per mm². This means that on an average 275-400 rods have to converge to a single neuronal cell leading to the visual centres, a figure representing an unusually high degree of spatial summation in the retina. In Tyto alba e.g. the ratio is only 15:1. In addition, the chorioidea of all Megachiroptera protrudes into the layer of rods in regularly distributed densely melanized cones (Fig. 2). On top of each cone a fine blood capillary loop emerges and penetrates deeply into the innermost stratas of the visual cell layer. Since the rods always point vertically to the chorioidea, the surface of the layer of rods looks regularly scrumpled, very much like an egg-container. Due to the large depth of focus gained by high refraction the resulting displacements of the rods by 75 μ from the top to the bottom of the cones do not impair the acuity of vision. The capillaries secure a quick blood supply and metabolic exchange on the receptor level. This may account for the adaptation within minutes when changing from daylight to dim twilight.

In numerous experiments based on a food reinforced training method I investigated the visual functions of Pteropus. The ability for brightness discrimination functions in the Flying Fox as well as in any other mammal so far investigated, and in man (Table 1). The visual acuity was measured as was the minimum separable of positive black and white stripes against negative homogeneous grey. It proved to be 18' in full light, a figure

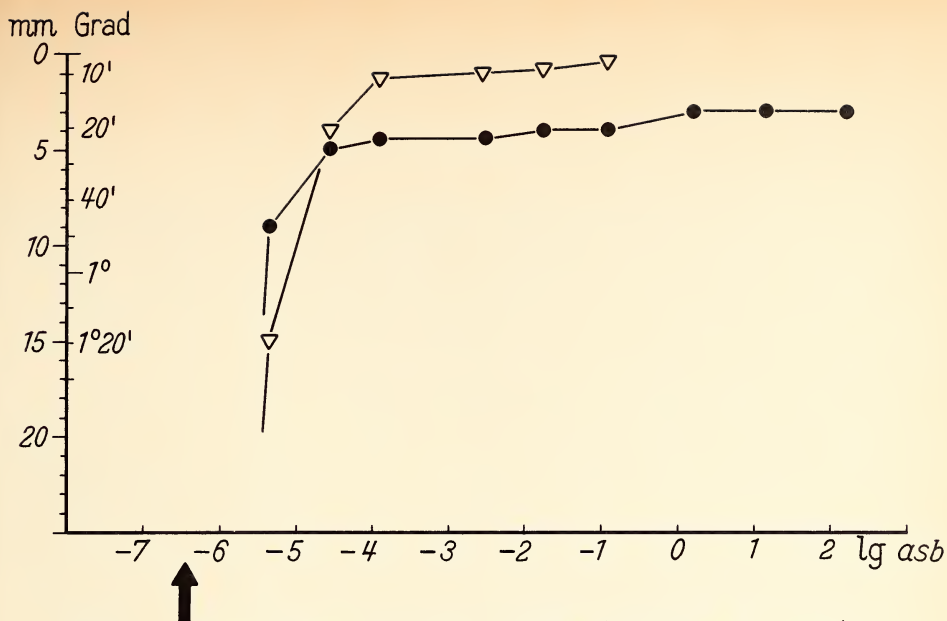


Fig. 3. Visual acuity of Flying Foxes (*Pteropus gig. gig.*)
 Abscissa: brightness in the experimental cage (asb).
 Ordinate: minimum separabile.
 Black dots: Flying Foxes, triangles: average of three male students, dash: threshold of visual perception in Flying Foxes

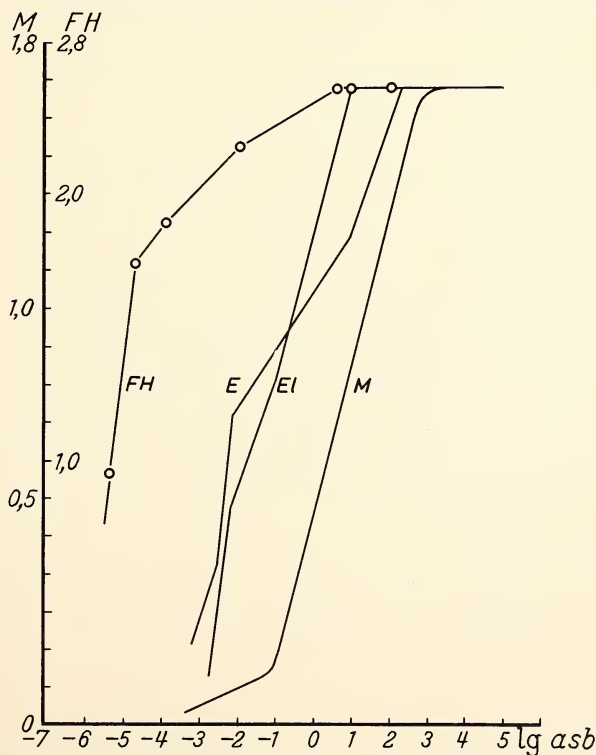


Fig. 4. Visual acuity in man (M), elephant (E), minnow (El) and Flying Fox (FH).
 Abscissa: Brightness in asb.
 Ordinate: 1/ minimum separabile.

equal to that of other nocturnal mammals, but much inferior, of course, to that in Primates (chimpanzee 26"). However, an examination of the visual acuity in steadily decreasing light produced a surprising result. Within the luminescence range of 100 to 0,1 Millilambert, where the visual acuity of man and diurnally active mammals sharply declines to nearly 1/10 of its best value, the visual acuity of the Flying Fox remains almost unchanged (Fig. 3). It slowly drops between 0,1 and 10^{-4} Millilambert. In the extremely dim light of 10^{-4} to 10^{-6} Millilambert the acuity of the Flying Fox is absolutely superior to that of man. In $4,5 \times 10^{-5}$ Millilambert the minimum separable of Flying Foxes was 48', whereas 3 students, measured under the same conditions only scored 1°20'! Thus, in extremely dim light Flying Foxes definitely see better than man. The absolute visual threshold was found to be less than $4 \cdot 10^{-6}$ Millilambert, roughly the same as in man and in owls. The investigation shows that in non-echolocating fruit-bats entirely sufficient orientation during night-time is still possible due to an eye that is perfectly adapted to vision in dim light. The same may be true for all Megachiroptera. Unpublished results obtained by KULZER disclose that Rousettus can see as well as Pteropus. Again, as in the case of Collocalia and Steatornis I would like to submit that in Rousettus echolocation is an adaptation to cave-roosting where absolute darkness may occur. During nocturnal activities vision may still be a major information source.

Microchiroptera.

In all the species discussed so far the importance of echolocation has somehow been downgraded. This is not the case with

Microchiroptera or insectivorous bats, animals which in addition to cave, roosting have turned to nocturnal hunting on the wing. The discovery by GRIFFIN (16) of echolocation in bats leads to an abundance of good papers on echolocation and hearing. But only little experimental research concerning other senses can be traced. Anyhow there is ample evidence that bats can orient themselves excellently by echolocation alone. GALAMBOS and GRIFFIN (17) showed that in a wire barrier experiment bats performed better when blindfolded. 28 Myotis l. lucifugus hit 1 mm Ø wires in 30 % of 3021 trials when untreated but in only 24 % of 2016 trials when their eyes were covered. This result indicates on the other hand that sighted bats may see crude movements of objects, and that these may distract their attention thus decreasing the rate of misses in the barrier experiment. CURTIS (6) tried to investigate the visual function of the eye of the bat: Ear-plugged Myotis l. lucifugus had to learn how to avoid white cardboard barriers, 5 cm in width and suspended 1,5 m below the ceiling. The space between the barriers was 30 cm. None of the 4 bats tested gave any indication of being able to see the choose between a lighted and a dark side of a cage. There was some evidence the bats followed the lighted one. Trials where they had to differentiate between stripes of a visual angle of 1° and others of 8° failed completely, so vision definitely does not play any part in orientation during cruising flights. EISENTRAUT successfully trained Eptesicus serotinus to crawl towards a white door and a black one. Only behind the white door was the bat able to find some food. Already after a few trials the bat had learned to

Moreover most of the nocturnally active rodents and insectivores only hunt within a limited territory which, after a few cautious exploratory visits, they know extremely well. There are numerous observations which indicate that all these vertebrates, including the echolocating ones, have an excellent memory of localities. An observer justly wonders how a cave-swiftlet can find its own nest out of a cluster of thousands within seconds. Many investigators of bats have observed how memory gets the better of echolocational evidence, e.g. when bats stubbornly try to enter a cage at the fenced frontside after the usual entrance has been turned to the back. NEUWEILER and MÖHRES have shown that the memory of Megaderma lyra functions with an accuracy of about 2 cm shifting limit. Shrews often store their food in certain spots, so they must have an exact remembrance of places in order to refind the store. Since memory is not a sense organ we will not discuss this problem further, but the importance of memory in the orientation system of echolocating terrestrial mammals cannot be overemphasized, and it is deplorable that this problem has only very rarely been investigated by experiments.

This review leads to the conclusion, that, apart from Microchiroptera, interaction of echolocation with other sensory organs - mainly with vision - is indeed an important factor in the re-orientation of echolocating terrestrial mammals. Or, to put it the other way round, only Microchiroptera so far have learned how to make full use of all the informative capacities implicit in echolocation.

The interaction may be classified as follows:

discriminate between white and black. Hitherto it even ran through a sequence of 4 differently placed white doors, completely disregarding the black ones. A training for discrimination of blue and yellow failed.

This year SUTHERS (41) in a very carefully planned experiment succeeded in proving that echolocating Microchiroptera are able to see moving patterns. In 9 species of American bats he could elicit optomotor responses to moving vertical black and white stripes presented to the bat on a rotating cylinder. By this method he measured the minimum seeable visual angle. The smallest stripes presented were seen under a visual angle of 0.7° (= $42'$) from the bat's central position: Saccopteryx leptura 0.7° , Phyllostomus hastatus 3.0° , Anoura geoffryi 0.7° , Carollia perspicillata 0.7° , Artibeus jamaicensis 3.0° , Desmodus rotundus 0.7° , Diaemus youngi 3.0° , Myotis lucifugus 6.0° . This investigation has two shortcomings. Firstly, those bats which still followed moving stripes of 0.7° may detect even smaller visual angles, since narrower stripes were not yet tested; secondly, SUTHERS did not measure the exact light intensity used which makes comparisons with other results difficult. Apart from experiments with Myotis the illumination was decreased, so that the experimenter barely could see the outlines of the bat. He used bulbs made for operation on 120 V on half the voltage only. This most probably resulted not only in an intended drop of intensity but also in a shift of the spectral composition of the light.

It is of interest to note that those species which still responded to small angles were either insectivorous, frequently hunting in the daytime (Saccopteryx), or fed on fruits, nectar

or non-flying vertebrates. On the other hand, Myotis, a purely nocturnal bat exclusively hunting insects on the wing, shows the poorest vision. This again is a hint that wherever vision is biologically feasible, even faint light is used as an information source.

Significantly enough there is no longer any correlation between light intensity and sound emission in Microchiroptera. In Megaderma lyra the sound intensity and the repetition rate did not change at all when the lights were switched off (31), yet optical cues are not completely disregarded e.g. we observed that newly caught Megaderma lyra when released for the first time in a room, invariably flew towards the bright windows and hit the glass at full speed. The brightness of daylight entering through the glass may be taken as a sign of an escape route. Similar observations were made by DAVIS and BARBOUR (7). They (2) and WILLIAMS, WILLIAMS and GRIFFIN (45) showed that homing in bats is adversely affected by blindfolding. There are numerous other observations indicating that bats use coarse brightness patterns in choosing dark roosting places or in looking for an opening in a cave. All investigators report olfaction to be poor in bats. Before the discovery of echolocation many scholars thought that the incredible skillfulness in nocturnal orientation might be due to an unusual sensitivity to air currents. But DIKJGRAAF (9) states that the sensitivity of their wings to mechanical stimuli is not superior to that in other mammals. SYCH (42) gave Myotis myotis a choice of 4 wind channels with air currents of different speed. Air currents of 0,2 and 2,5 m/sec were most attractive to unfed bats, whereas well fed species remained indifferent to wind speed. That means that air currents may occasion-

ally and for a limited time contribute some cues to spatial orientation.

Rodents and Insectivora.

In the last group of animals we are going to discuss, the occurrence of echolocation is still disputed. In 1951 KAHMANN and OSTERMANN (22) reported jumping-experiments with golden hamsters, shrews and dormice in darkness. The results of the experiments suggested that these mammals used echos in locating a small and unreachable platform. BROTZLER (3) repeated this experiment with golden hamsters and denied any echoorientation. He failed to detect any sound production using a mike built into the platform on which the hamsters had to jump. In a very extensive study he comes to the conclusion that golden hamsters preferably use optical signs for orientation in dim light down to 9.10^{-5} Millilambert and that the use of olfactory signs comes second. In reorientation space memory is a major factor.

ANDERSON (1) reported lab-rats to emit pure inaudible tones between 20 and 30 kHz/sec. and audible sounds containing overtones of up to 80 kHz/sec. In RILEY's and ROSENZWEIG's (36) experiments enucleated rats had learned in 84,3 % of the trials to avoid from a certain distance a pathway closed by a metal sheet barrier and to use the open one instead. When the barrier was put at 45° they scored only 54% correct. The performance increased immediately when the barrier was turned back to 90° . The substitution of cloth sheets for the metal barrier resulted in a decrease down to 51,8 %. When the barrier was put at an angle of 135° a mike indicated that more echo returned from the open pathway, and indeed the blind rats avoided the free pathway in 60 % of

20 trials. When hearing was impaired by puncturing the eardrums the performance dropped sharply to 55,5 %, though this is still above chance level. In my opinion these results do not prove conclusively that rats use echolocation, especially since the authors state: 'Vocal sounds of the rat, whether audible or ultrasonic, are produced infrequently in the maze and they do not seem to be related to maze performance'. The authors suggest that rats use noise which is produced unvocally, but in this case we can no longer speak of echolocation in the proper sense of the word. Furthermore, we cannot exclude the possibility that the blind rats used some olfactory signs or even noticed the barrier by body heat reflection from the metal sheet. TSANG (43) found that in an open maze sighted rats learned more readily than blind ones, but that in a closed maze enucleation had no effect. This indicates, according to his opinion, that echolocation may be involved in orientation in a closed maze. Anyhow blind rats performed worse than sighted ones, and since the experiments carried out by LASHLEY (24) we know that rats in dim light have good vision. HERMANN (20) published a paper on the physiology of vision in pigmented rats. It took his rats only 1,5 min to adapt from daylight to 0,22 Millilambert. They could easily distinguish between vertical and horizontal stripes, and stripes of an obliquity of 60° and 30° . Their optimal visual acuity measured 20'. The upper flicker frequency ranged from 35-40/sec. The morphological features and the dioptrical device revealed an eye that is adapted to night vision. The similarities between that eye and that of the Flying Fox are striking. GREENHUT (14) showed that rats can distinguish a peg put at a distance of 25 cm

from a peg placed at a distance of 32 cm. Numerous visual cliff experiments (4) with rats confirm the fact of good visual depth perception. They are also thought to be macrosmatic, but studies of GRUCH (19) on olfactory thresholds in rats revealed values not lower than in man. The thresholds for acetic acid, propionate and valeric acid were in a range of 10^{12} to 10^{13} molecules/cm³ air as compared to thresholds of 10^4 to 10^5 in the dog.

In shrews echolocation is claimed to occur in experiments made by GOULD (12) with Sorex palustris, S. vagrans, S. cinereus and Blarina. Gould reported that shrews emitted very weak and short ultrasonic sounds whenever they were searching the rim of a disc for an escape platform which was placed on a lower, unreachable level. With olfactory signs and light completely excluded Sorex successfully jumped on to a platform in 75 % of 12 trials (per chance level: 8 %). Ear-plugged shrews however refused to jump 2 times in 7 trials. They missed 3 times and jumped successfully 2 times. This means that 28 % of the trials were still positive, a result significantly above chance level, if chance level means anything in a set of a dozen of experiments. In our laboratory Grünwald (not yet published) repeated Gould's experiments and blinded shrews jumped onto the lower platform as successfully as hearing ones.

Nothing is known about the function of other sensory organs in shrews. SHARMA (39) maintains that the retina of Suncus murinus is not degenerated. According to his description cones are missing whereas elements resembling rods can be seen. He does not hesitate to conclude that the sense of sight is very poor in these animals.

Without ever mentioning the reasons for his conclusions CROWCROFT (5) states that shrews are very shortsighted. He describes olfaction as being very poor, too. According to his observations shrews find food mainly by touch, the long fibrissae fanning outwards and forwards from the muzzle.

Recently GOULD (13) described echolocation in tenrecs (Hemicentetes semispinosus, Echinops telfairi, Microgale dobsoni) by the same methods he had used with shrews. Tenrecs produce short tongue clicks of a frequency of 15 - 17 kHz/sec. The arguments used in the discussion on the shrews are valid for tenrecs, too. Gould mentions that Centetes turns its head when following the approach of a hand, whereas with Hemicentetes and Echinops the same experiments produced no apparent response. He thinks it possible that Centetes uses a combination of vision and echolocation. EIBL-EIBESFELDT observed tenrecs marking their way by odorous secretions. Olfaction therefore certainly plays a part in orientation.

Some other terrestrial mammals are suspected to use echolocation: Dormice, mice, Cynecephalus (Dermaptera), Erinaceidae, and Echidna, but so far nothing has been proved experimentally.

With the exception of some extraordinary situations, e.g. the sounding of cliffs or fissures I cannot see how echolocation can be of any advantage to mammals living close to the surface such as rats, shrews and tenrecs. In the natural habitat of these animals grass, shrubs and so on are always near and often within reach of the vibrissae and of the sensitive snout. So the sense of touch and also olfaction certainly are important sensory inputs for environmental orientation.

- 1) Substitutional cooperation. The use of echolocation is reversely correlated to the intensity of the light available. This is the case with Collocalia and Steatornis, and to a lesser degree with the fruit-bat, Rousettus.
- 2) Simultaneous interaction. Here we have to distinguish two groups:
 - a) Echolocation is the predominant means of orientation, other sensory organs having only auxiliary functions. So far only the Microchiroptera can be put into this group.
 - b) Echolocation is not predominant, and may be used under special circumstances only. Shrews, tenrecs and possibly rats may belong in this group.

Because of a certain lack of experimental evidence this review contains many speculative statements. If we are to reveal not only the mechanism of echolocation, but also the interacting processes of the strikingly successful orientation of nocturnal vertebrates, we will have to stop looking only at the sense organs. Instead, we ought to begin with investigations into the processing mechanisms of sensory data in neuronal centers where the true problems of orientation start.

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PERCEPTION AND DETERMINANTS
OF UNDERWATER VOCALIZATION
IN THE CALIFORNIA SEA LION

by
R.J. SCHUSTERMAN¹

I. Introduction

The California sea lion (Zalophus californianus) is the best known of all the sea lions, appearing as the trained "seal" in most zoos and circuses all over the world. It is a carnivore and belongs to the Family Otariidae of the Suborder Pinnipedia (55). These marine mammals are characterized by having an external ear or pinna and a hind-flipper which can be turned forward for either standing or for purposes of quadrupedal locomotion (34). The fore-flippers are large and are the primary means of propulsion in swimming (15).

The first systematic account of all the pinnipeds to be published within the past 50 years is the book by Scheffer (55) entitled Seals, Sea Lions and Walruses. The author, who cites some 500 references, shows clearly that we know a good deal about the morphology, ecology and distribution of these animals and something of the physiology of certain selected species. In addition, due primarily to the efforts of Bartholomew and his associates (6,7,8), we know something of the social behavior of the northern fur seal and the northern elephant seal during the breeding season. Yet, in spite of this, our information about the sensory and behavioral capacities of seals and sea lions is extremely meager. Thus pinnipeds in general, and specifically the California sea lion, have been a neglected group of animals in the

area of comparative animal behavior and should be studied more assiduously, both in their own right and especially if we are to place the behavioral capabilities of other marine mammals, such as the whales and porpoises, in proper perspective.

In view of recent research activity and discussion on the sonar or echolocation capabilities of the bottlenose porpoise, Tursiops truncatus, (32,47,48) its vocal and communicative abilities (2,16,38,39), and its visual and auditory perceptual abilities (30,32,56), it behooves the student of animal behavior to run parallel studies on other marine mammals (e.g., seals and sea lions) having grossly different sensory and brain structures from those of porpoises. A start in this direction has been made by the author and forms the substance of this paper.

Since it has been firmly established that the bottlenose porpoise possesses an extremely efficient biological sonar system, it is reasonable to suspect that other marine animals may also be so endowed. As Schevill, Watkins and Ray (57) have pointed out, although little is known about the sea lion's olfaction, audition and vision, what is known about their ecology suggests at least an expert passive use of sonar (listening), if not an active use of sonar (echolocation) for purposes of navigation and finding food.

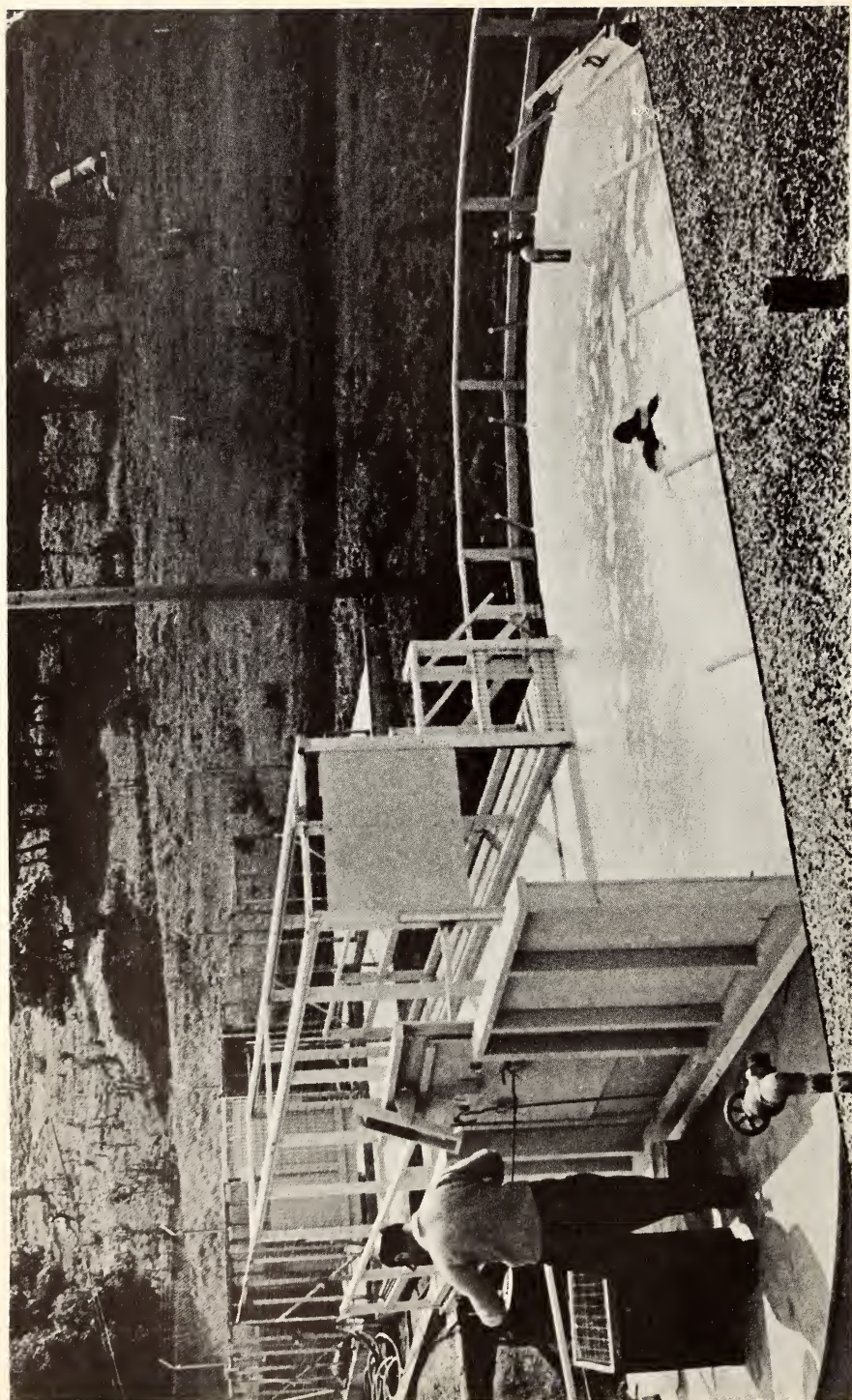
II. The Present Approach

A. The Problem

The initial impetus for these studies was Poulter's report (50,51) that the emission of "sonar" clicks by Zalophus enabled it in total darkness not only to detect pieces of dead fish but also to discriminate between a piece of fish and a piece of horsemeat of approximately the same size. However, as our initial exploratory studies were undertaken,

it was soon apparent that if Zalophus had a sophisticated sonar system, its properties and functioning were much more elusive of demonstration than had originally been suggested by Poulter. Initial observations indicated that the California sea lion was primarily a visual animal. Furthermore, in contrast to the Atlantic bottlenose dolphin (32,48), the "sonar" pulses which were initially elicited from our young captive sea lions were indeed scanty. Thus, it was reasoned that the operation of Zalophus' sonar system, if indeed one exists, ran more along the lines of the oil bird, Steatornis caripensis (25), or possibly the fruit-eating bat, Rousettus (26). These animals orient themselves visually when light is present, but depend on easily audible clicks in the absence of visual cues. The most logical approach, therefore, was to find out something about Zalophus' sensory abilities and to determine under what conditions "sonar" clicks could be elicited.

Since there was virtually no information in the literature regarding the sensory capacities of Zalophus, preliminary studies of their visual and auditory perceptual capabilities were of primary concern. Concurrent with these studies a major effort involved the development or search for a model or concept which would facilitate understanding the causes of Zalophus' production of underwater clicking vocalizations as a general phenomenon, rather than as the first stage of a highly efficient biological sonar system. The most widely applicable approach was to view clicking as part of a single system of vocalization or calling. Furthermore, such vocalizations were considered as one component of the "orientation reflex" or "alerting responses" in general which may be evoked by a complex of stimuli relevant to such states of high muscle tonus and autonomic activity (3,4,5,9,66). This approach was modeled after that of Andrew who has developed the concept of "stimulus



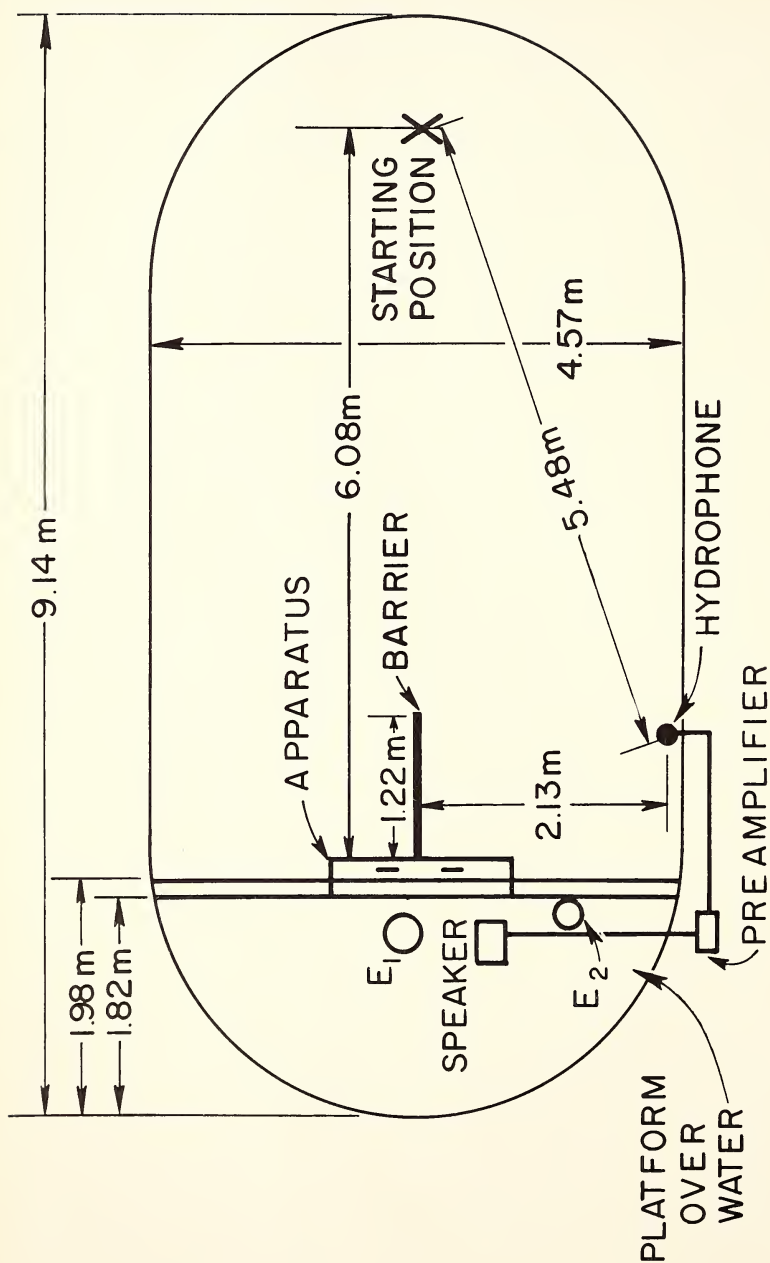
1. A sea lion in the experimental tank waiting for a trial to begin.
The experimenter is in the process of changing targets.

contrast" to account for the vocalizations of chicks and nonhuman primates. According to Andrew, "calls appear to be elicited by any stimulus that by its inherent properties or by valency given by conditioning is capable of arousing intense or prolonged attention. Such stimuli are said to possess 'contrast'. The more intense the contrast, the more intense is the resulting call." (3, p.315).

B. Methodology

All experiments except those dealing with underwater hearing were conducted in an oval tank, constructed of redwood and measuring 4.6 m by 9.1 m and 1.8 m deep. The interior of the tank was painted white; during testing it was filled with 82 kl of fresh water, and animals could be observed and photographed by means of six windows spaced around the perimeter of the tank.

Generally, two types of procedures were used. The first was a discrete-trial procedure in which various kinds of stimulus targets in a fixed position were submerged from the testing platform shown in Fig. 1. The experimenter (E) worked from behind an opaque screen which was set out 15 cm from the dock area and extended down to the water line (see Fig. 1). Unless otherwise indicated, two targets were presented simultaneously so that they projected below the opaque screen and were at least 38 cm below water level. At the beginning of a trial, a stimulus panel located behind the opaque screen was lowered to the water level. Attached to the side of the stimulus panel facing the E were two rods, 1.1 m in length and 0.64 cm in diameter. The targets were attached to the lower portion of each rod by means of set screws. Deflection of either rod activated a microswitch which produced an audible click as well as a light signal behind the stimulus panel. A perpendicular divider of mesh wire projected down to the floor of the tank



2. Schematic diagram of the experimental tank showing the starting position of a sea lion during the discrete-trial procedure. Locations of the recording equipment and test apparatus are also shown.

and 1.2 m outward from the opaque screen, thus lying between the targets and preventing the animals from moving laterally from one target to the other. The distance between the centers of any two targets was 57 cm. A schematic diagram of the testing situation is shown in Fig. 2.

During testing, the sea lion's task was to push one of two targets in order to obtain a small piece of herring (Clupea pallasii) weighing approximately 5 gm. The E immediately reinforced a correct response by dropping a piece of herring through a 16 cm gap situated between the opaque screen and the testing platform. The stimulus display was immediately withdrawn following either a correct or an incorrect response. The position of the target was an irrelevant cue, i.e., it was randomly determined, throughout all the experiments to be described. In addition to errors or correct responses, the principal behavioral measure under this procedure was the presence or absence of a train of clicks on any given trial. A trial began when the stimulus display was submerged and terminated when it was withdrawn from the water.

The second procedure may be called a free-swimming procedure. Typically, an animal was introduced into the tank and two Es made observations from the testing platform by means of a time-sampling technique. This procedure enabled E to obtain a minute-by-minute quantitative record of each sea lion's specific behavior patterns including underwater vocalizations. The details of this technique are outlined in Section VI, E.

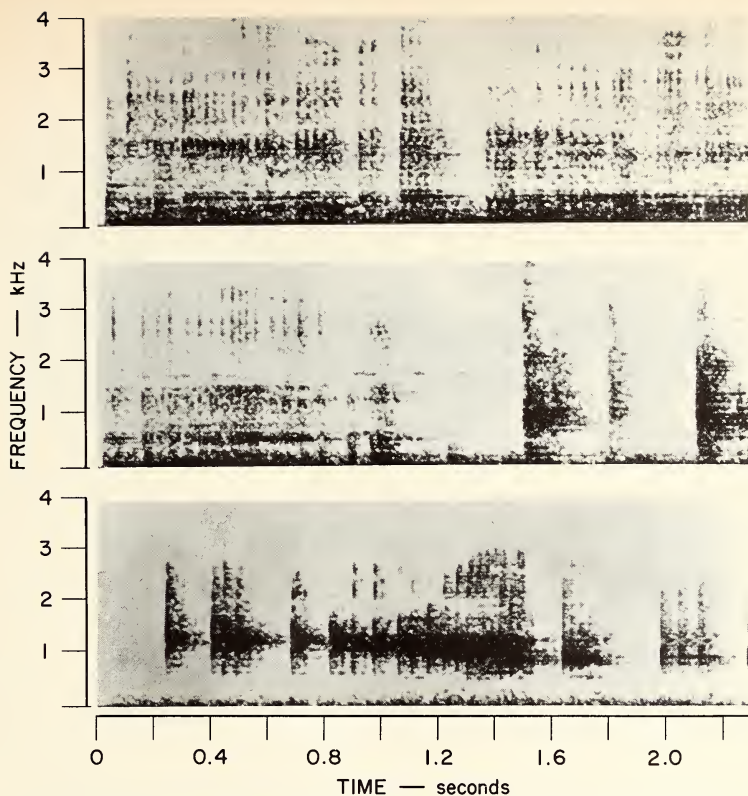
Throughout the entire research effort, underwater vocalizations were continuously monitored by a Channel Industries 275 hydrophone (20 Hz to 150 kHz) and an Ampex 2044 amplifier-speaker system (65 Hz to 13 kHz). Vocal signals were periodically recorded on a Uher 4000-S tape recorder at 20 cm/sec. (40 Hz to 20 kHz) and were analyzed by a Kay 661 audio spectrum analyzer or sonograph.

III. Underwater Sound Production

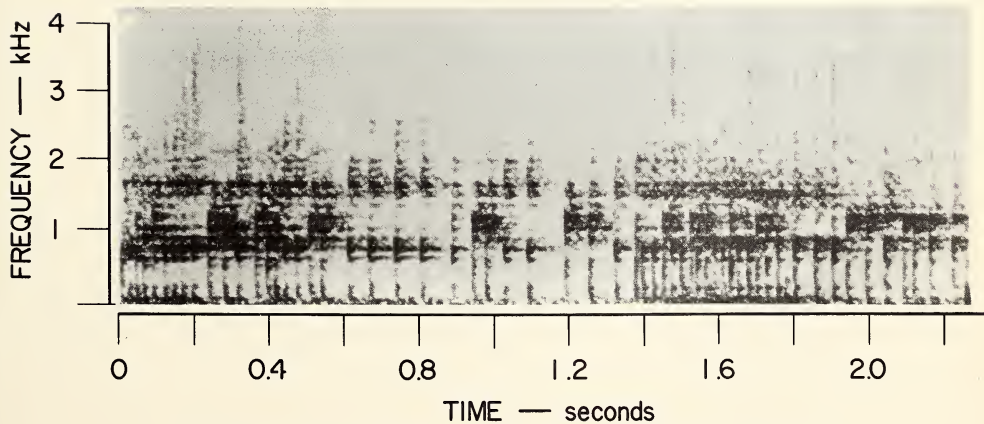
Although it has long been known that cetaceans, especially the porpoises, are capable of producing different kinds of underwater sounds (32), observations of the sea lion's underwater sound production has only recently come to light (50). The California sea lion, thus far, has been especially implicated in the emission of two types of underwater sounds--clicks or short-duration sound pulses and barks (57). In contrast, the bottlenose porpoise has been reported to produce a wide variety of sounds which have been generally categorized as clicks, whistles or squeals, barks (20) and "cracks" (14). Although the clicks have been primarily implicated as the sonar signal of the porpoise, there is good evidence indicating that a variety of whistles have emotional and communicative significance. Some whistle contours and the cracking sounds have been shown to be associated with distress or fright reactions (14,40).

On the other hand, underwater clicks by Zalophus have been reported to occur usually when an animal was in the final stages of searching for food (50,57) or for an object signalling food (19,59). Most of these tests have limited the range of behavior to those involved in feeding activities. In order to determine whether Zalophus is capable of emitting a greater variety of underwater signals and calls than previously reported, several sea lions were monitored while swimming freely under a number of stimulus conditions, including novel or strange objects and social interactions (see Section VI, E for a more detailed account of the stimulus situations).

Sonograms of the evoked signals were made, using the Kay sonograph. This technique provides a graph of frequency against time, with the intensity of each frequency-band shown by the darkness or density of the



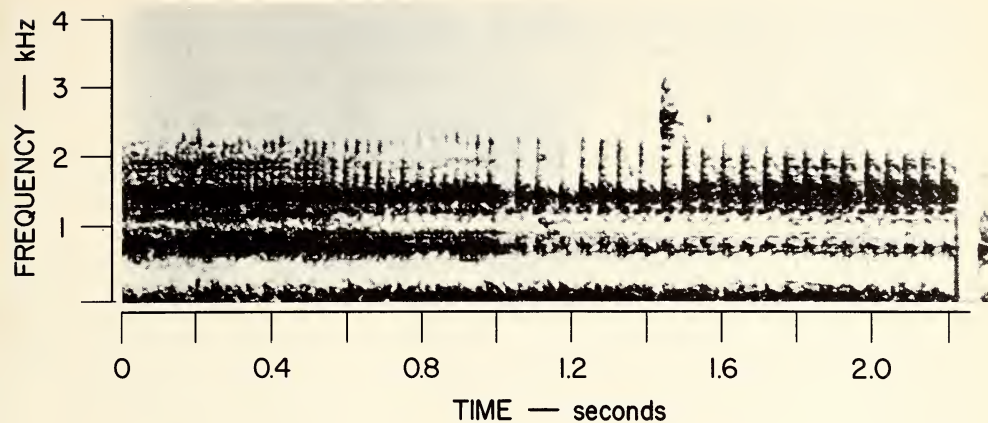
3. Sonograms sampling a continuous series of clicks emitted by a 3-yr-old female California sea lion (Bibi) while apparently searching for live fish in very turbid water (narrow band).



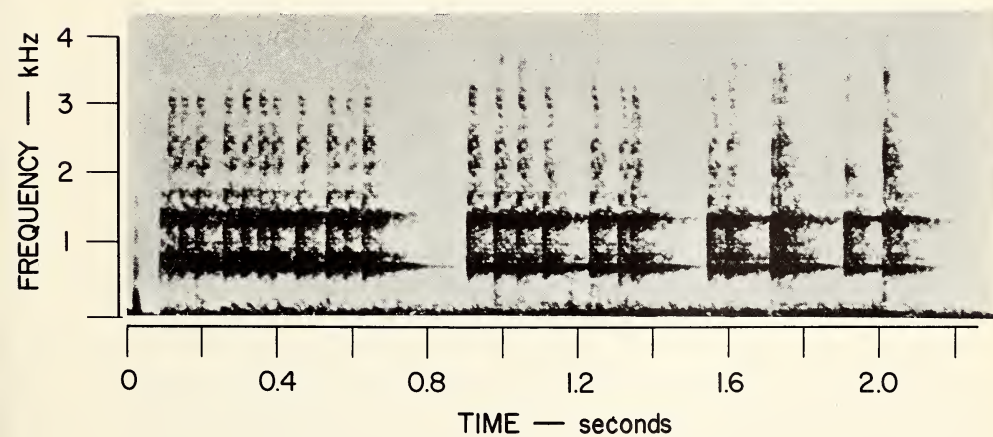
4. Sonograms of clicks emitted by a 3-yr-old female California sea lion (Cathy) while play-fighting with another sea lion (narrow band).

paper markings. Either of two analyzing bandpass filters (narrow or wide) may be used with the Kay sonograph. The wide-band filter has an effective bandwidth of 300 cycles, and the narrow-band filter has an effective bandwidth of 45 cycles. The analysis used is indicated on each of the sonograms presented. The use of this method for the analysis of biological sounds has been described by Borror (12).

Clicks. From our analysis, and as is apparent from a careful inspection of the sonograms illustrated in this section, Zalophus produces almost an infinite variety of click patterns. Although most of the click trains have a duration of 2 sec. or less, many trains last as long as 23 sec. with pauses of less than 0.5 sec. A few clicks are merely very narrow columns of "noise", i.e., without harmonic structure (e.g., sonograms b and c shown in Fig. 3). Most, however (e.g., Fig. 4), are composed of a fundamental and at least one harmonic. In the sonograms shown the dominant frequencies range from below 500 Hz to as high as 1200 Hz with components only slightly above 4 kHz. The click repetition rate may vary from less than 5/sec. to 70 or 80/sec., all within a given click train (separation between clicks of 0.5 sec. or less). Figure 3 presents a particularly interesting series of clicks. The sonograms show a sample of 7.2 sec. of a continuous series of clicks lasting approximately 22 sec. The sea lion (Bibi) produced this series while apparently searching for live mudsuckers (Gillichthys mirabilis) under extremely poor visibility conditions (see Section VII, B). The figure shows the beginning of the click series (a) which had some very low frequency components with a repetition rate of about 50 clicks/sec. During the middle of the series, there was a short pause (b) followed by two high energy "cracks" or "bangs".



5. Sonogram of clicks emitted by a 4-yr-old male California sea lion (Growler) while swimming freely in clear water (narrow band).



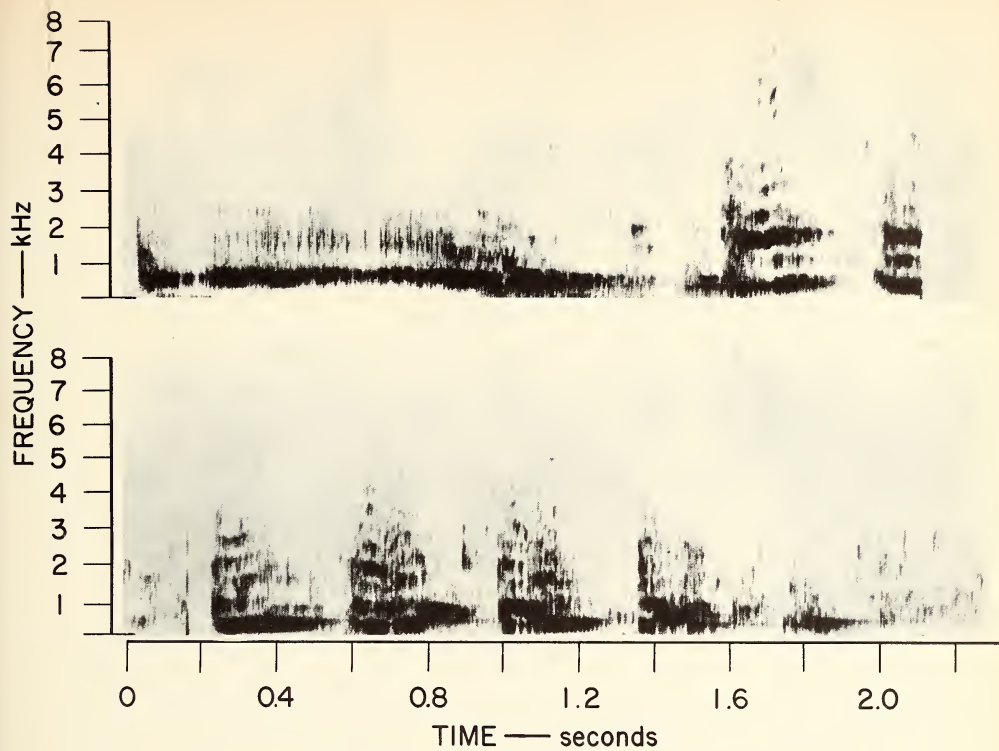
6. Sonogram of clicks produced by a 3-yr-old male California sea lion (Sam) while swimming in the presence of a mirror stimulus (see Section VI, E of text) (narrow band).

Subsequently another short pause occurred and clicking resumed with the dominant frequency at 1250 Hz (c) and a pulse rate as low as 10/sec. Although all the initial clicks covered a frequency spectrum of about 4 kHz, some clicks toward the end of the series showed rather systematic changes in frequency ranges (shown in c); some had a frequency range of less than 1500 Hz.

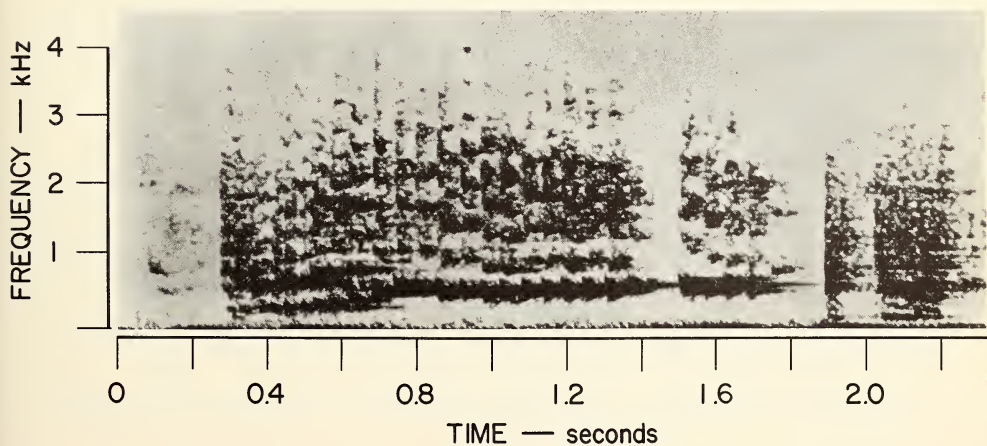
Figure 4 is a sonogram of clicks produced by one sea lion while play-fighting with another sea lion. When the tape which produced this sonogram was replayed, I noted that a popping sound seemed to be superimposed on the clicks. This is indicated on the graph, I believe, by the great variation in the frequency pattern. Such a sound pattern is highly distinctive and has been produced by only one of the animals (Cathy). Figures 5 and 6 present underwater clicks emitted by two male Zalophus and are indicative of two other types of click patterns.

It is important to note that clicking sounds were never emitted at fairly regular intervals by any of the animals under any of the free-swimming conditions. This is in marked contrast to the bottlenose dolphin, which is reported to emit "exploratory" pings every 15 to 20 sec. (32). Such periodic signal emission has been suggested as the sonar equivalent to "glancing" in the field of vision (32).

Barks. This form of underwater vocalization has most of its energy below 3500 Hz, although some energy may be found at frequencies as high as 8 kHz. There is little variation in the duration of any given bark--they generally last from 200 to 300 ms. Barks are sometimes preceded by a series of clicks, as shown in Fig. 7. The sounds shown in this figure were produced by a two-year-old male Zalophus while it was fleeing from the E who was attempting to drive the animal out of the testing tank. During E's initial attempts, the animal swam rather rapidly



7. Sonograms of clicks and barks produced by a 1.5-yr-old male (Tommy) while fleeing from the experimenter (wide band).



8. Sonogram of Bibi's "whinny" vocalization produced during an aggressive encounter with another California sea lion (see Section VI, E of text) (narrow band).

while producing long trains of clicks. As the action became more intense, the clicks shifted into a series of barks. The shifting from clicking to barking under these circumstances suggests that the two types of calls form a single system of vocalization which changes as a function of the level of arousal, with barking indicative of a higher level of arousal than clicking.

"Whinny". A sonogram of this vocalization is shown in Fig. 8. It was frequently produced by a 3.5-year-old female Zalophus (Bibi) during an aggressive encounter. For lack of a better term, we have called it the "whinny" sound since it sounds a little like a horse neighing. This vocalization is often preceded by clicks or a growl sound. The whinny typically lasts for about 1.5 sec. and may be repeated three or four times in succession. The sonogram indicates a fundamental at 500 Hz with harmonics to 3 kHz. The marking on the extreme right of the graph is a water noise. This whinny sound may be the female counterpart of a male bark. However, contrary to another report (11), I have heard females bark both in air and submerged.

"Buzzing". A characteristic "buzz" sound from a sea lion in a social situation is depicted in Fig. 9. This vocalization may actually be a series of discrete sound pulses which occur so rapidly that they take on a buzzing quality.

"Bang" or "crack". This sound has thus far been produced by two of our California sea lions (Bibi and Sam). The sound was first heard when Bibi was confronted with its mirror image and was repeated several times over a period of days, usually under the same circumstances. Figure 10 shows a pair of these high-energy "bang" sounds. The sound, which has always been associated with very rapid swimming, appears quite loud and mechanical to the human ear, and, as the sonogram shows,

it is a broad-band pulse with a rapid onset. Apparently, from the description of Caldwell, Haugen and Caldwell (14), Zalophus' "bang" sound is very similar to high-energy "crack" sounds produced by Tursiops truncatus under conditions of fright. We have recently heard similar sounds produced by the Steller sea lion (Eumetopias jubatus) while performing on an underwater visual discrimination task. It is not clear how the "bang" sound of Zalophus is produced, i.e., whether it is made by the sea lion's vocal apparatus, by jaw-clapping, or by some other mechanism such as the front flippers causing an underwater cavitation as they are thrust together and then parted during initiation of a very rapid swim.

Sound production mechanism. Careful observations of Zalophus while it was in the act of emitting underwater clicks have indicated some movement in the area of the throat or larynx; such movement appeared less pronounced when the animal was silent. These preliminary observations implicating the laryngeal area as the underwater sound-producing site of Zalophus have been supported by experimental evidence (T. C. Poulter, personal communication). Using a triangulation technique, Poulter found that the site of underwater barking was the vocal cords on the anterior portion of the larynx and that the apparent point of origin of underwater clicks was posterior to the vocal cords.

All of the underwater vocalizations that have been described can apparently be produced with the mouth and nostrils closed and therefore without the emission of bubbles, or with the mouth and nostrils partially opened and with the emission of bubbles. Moreover, clicks may be produced in air with the mouth closed or with the mouth wide open. Barking sounds seem to show the same basic frequency-intensity structure in air and under water. However, clicking in air is usually less intense and much less

frequent than under water. Although no systematic attempt has yet been made to measure the intensity of Zalophus' underwater clicks, there has been no difficulty in monitoring these sounds even when the background noise was considerable and the animal was as far as 5 to 6 m from the hydrophone. This contrasts with the findings of Schevill, et.al. (57) who state that the underwater sounds of Zalophus were so faint they could not be detected unless the animal was within 3 m of the transducer.

Although there are certain similarities between the sonar signals of the porpoise (Tursiops truncatus) and the clicks of Zalophus californianus, there are also great differences. Whereas the clicks of the porpoise are very narrow columns of noise having their greatest energy up to 30 kHz with smaller energy fractions to 170 kHz (32,47), those sampled from Zalophus thus far often contain a harmonic structure having their greatest energy at 500 Hz to 4 kHz with possibly smaller energy fractions at higher frequencies. Furthermore, regarding the porpoise, Norris reports that "during fine discriminations where sight is impossible, the environment is literally saturated with tiny plosive clicks, up to 500-600 per second." (47, p.320). Such rapid pulsing has not been consistently produced by Zalophus.

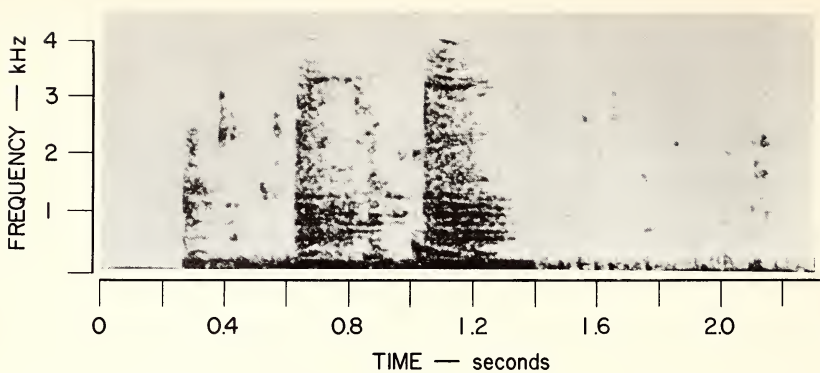
Since a higher vibration rate or sound frequency results in a shorter wavelength between a single compression and rarefaction and therefore a more precise resolution from a reflected echo, the porpoise is theoretically capable of much finer detections and discriminations by means of active sonar than is Zalophus. In fact, by this reasoning, on the basis of the sonograms presented here, Zalophus would be limited to the detection of objects at least 30 to 60 cm in diameter.

IV. Underwater Sound Perception

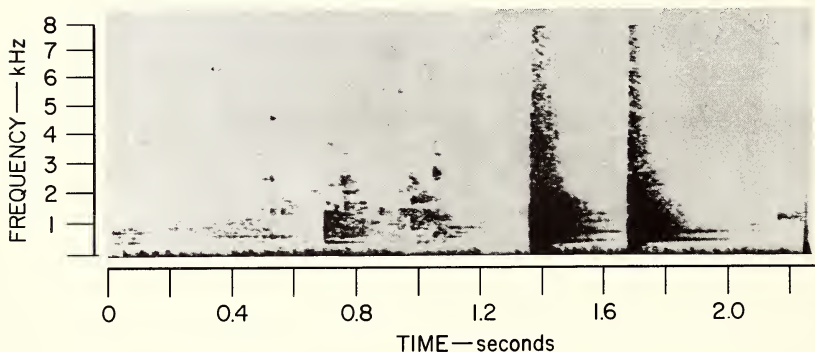
Both Scheffer (55) and King (34) indicate that there is no information of an experimental nature regarding the underwater or in-air hearing of Zalophus, or for that matter of any pinnipeds. There has even been some suggestion that their underwater hearing is "somewhat feeble" (11). However, the general belief of most investigators working with pinnipeds has been that, as in cetaceans, hearing is a very important sensory avenue in seals and sea lions. Our own general impressions tend to support this view. On several occasions, brief sounds have inadvertently been introduced into a testing tank with a submerged California sea lion or harbor seal, invariably resulting in the animal's orientation to the sound source.

In contrast to the very high-frequency hearing of the Atlantic bottlenose porpoise--shown to range between 75 Hz to 150 kHz with peak sensitivity at 50 kHz (30)--preliminary work at our laboratory and by William E. Evans (personal communication) indicates that the upper frequency range of underwater hearing of Zalophus is considerably lower and lies somewhere between 40 and 50 kHz.

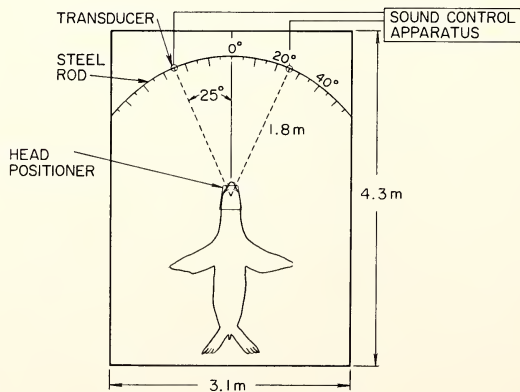
Recent investigations (21,53) on the anatomy and physiology of the cetacean acoustic mechanisms indicate that they are superbly adapted for purposes of underwater hearing with respect to both spectral or frequency analysis and auditory space-perception. A comparable anatomical analysis has yet to be worked out for the pinniped auditory mechanisms. On the other hand, behavioral tests of sea lion's underwater directional hearing, or auditory spatial perception, similar to those conducted by Dudok van Heel (17) with the porpoise, Phocaena phocaena have been conducted at our laboratory by Roger Gentry (23).



9. Sonogram of a "buzzing" sound emitted by Cathy while swimming with another California sea lion (narrow band).



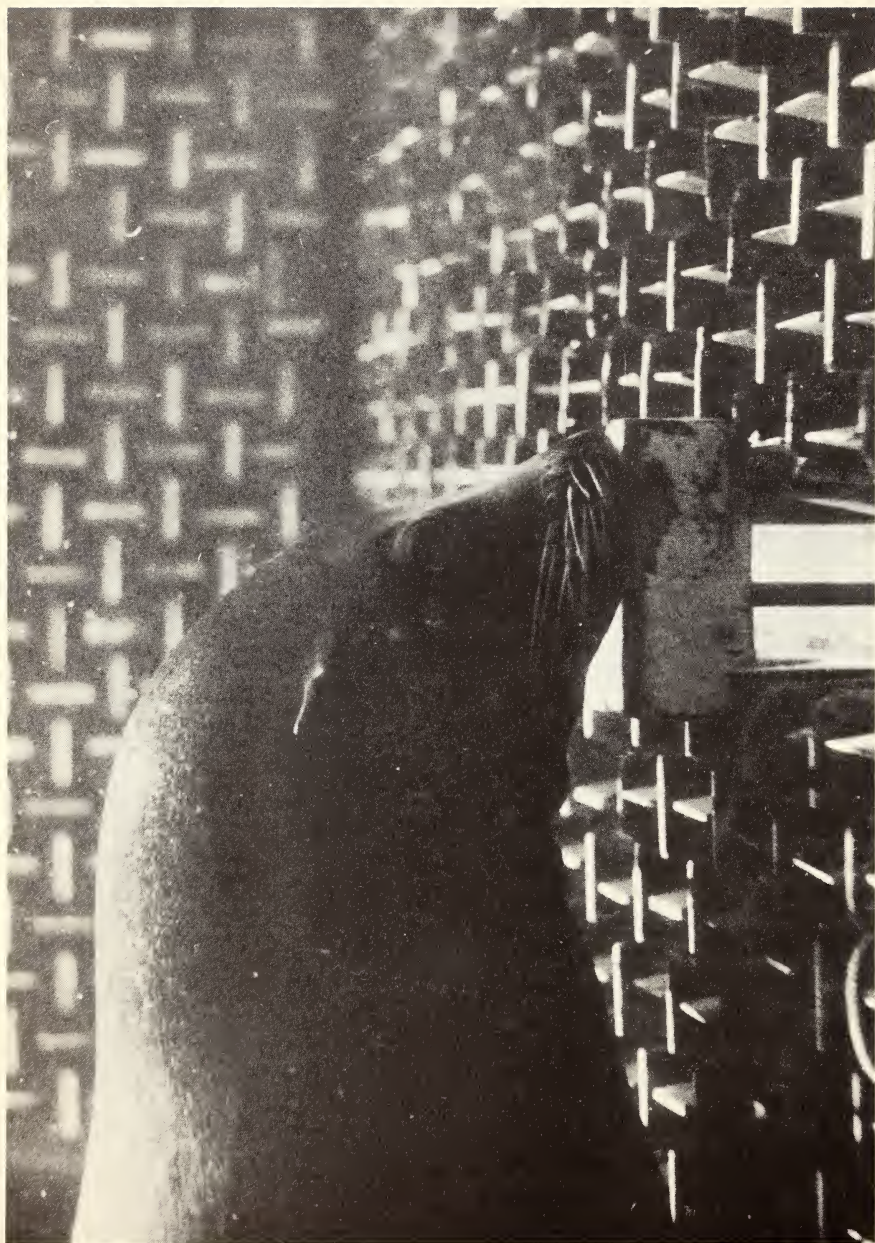
10. Sonogram of two "bang" sounds produced by a 3-yr-old California sea lion (Bibi) while orienting to a submerged mirror (narrow band).



11. Schematic diagram of the tank used to test hearing; shows locations of the sound transducers in regard to position of the sea lion's head.

These tests were carried out in a tank approximately 4.3 m x 3.1 m and 1.5 m deep, made partially anechoic by the placement of 15-cm-long wooden wedges along the walls and floor. At one end of the tank, two barium titanate transducers were suspended 60 cm into the water from a curved metal rod atop the tank. The rod was marked at 5° intervals from 40° left to 40° right azimuth. The median plane of the sea lion's head corresponded to a perpendicular dropped from 0° azimuth. These markings refer to the auditory angle defined as the angle subtended by either of the transducers from the center of the sea lion's head, which was maintained at a fixed position (see Fig. 11). The transducers were attached through a two-place selector switch to a MacIntosh 75-watt amplifier and an HD Model 200 cd wide-band oscillator. A rheostat placed between oscillator and amplifier acted as off-on switch and loudness control for the transducers. To give tones of standard loudness, an Eico Model 460 oscilloscope was attached to a hydrophone hung in the position where the animal's ears would be at the outset of each tone presentation. A rheostat setting was then selected for each frequency and transducer which would give a wave of standard amplitude on the oscilloscope. This was done before each test session. The sound level was + 1 dB (reference 2×10^{-4} dynes/cm²). To initiate a tone, E selected a transducer and then turned the rheostat quickly to the selected setting and back to zero. Of 90 measured tones produced by this method, 81% had durations between 0.3 and 0.4 sec.

The subject (Growler), a 4-year-old male Zalophus, was trained to lie in a fixed position on the bottom of the tank 1.8 m from the transducers with its head on a wooden block (see Fig. 12). The two-choice discrimination method was used, and the animal was trained to respond to a tone from one of two transducers by swimming to and nose-pressing the manipulandum (a round metal target) spatially contiguous with the

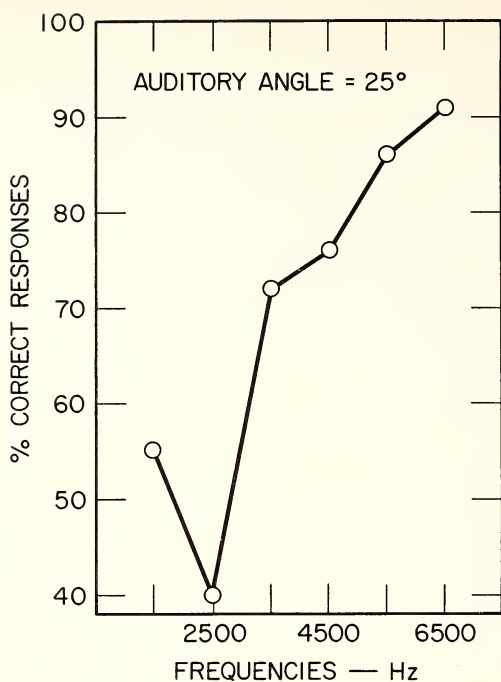


12. A sea lion positioning its head on a wooden block at the bottom of the "anechoic" tank during a test trial of its underwater directional hearing.

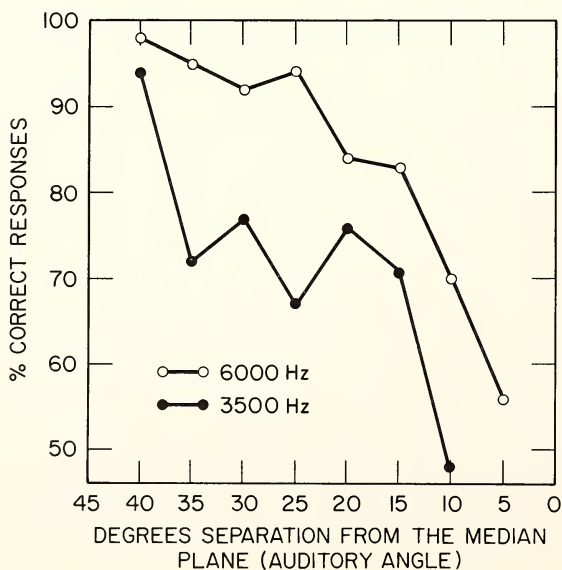
transducer. A correct response consisted of pressing the manipulandum associated with the activated transducer. Each such response was reinforced with a small piece of herring. Errors were never reinforced and a trial terminated with a target press. Activation of the right or left transducer was randomly determined.

As a preliminary step, the psychophysical method of limits was used in order to obtain a range of auditory angle settings with a constant tone of 6 kHz. Following this, formal tests were made by the psychophysical method of constants with tones of 6 kHz and 3.5 kHz. On the basis of the preliminary results, eight auditory angle settings were selected, ranging from 40° to 5° in intervals of 5° . Six such settings were presented for 15 consecutive trials at each test session until a total of 105 trials had been presented at each of the eight auditory angles. Randomized sequences of settings were given from session to session. The results of this experiment are depicted in Fig. 13, which shows correct responses as a function of auditory angle with frequency as a parameter. The results indicate that the California sea lion can reliably locate an underwater sound source at a minimum auditory angle of 10° when a 6 kHz tone is used, and at 15° when a 3.5 kHz tone is used.

In order to test hearing directionality over a wider frequency spectrum range, a second experiment was conducted in which the auditory angle remained at a constant 25° and the frequency varied from 1.5 kHz to 6.5 kHz in increments of 1 kHz. Again the psychophysical method of constants was used with six frequency settings presented for 15 consecutive trials at each test session until a total of 105 trials had been presented at each frequency. The results, illustrated in Fig. 14, show that at a constant auditory angle of 25° , performance of the California sea lion improved as a direct function of increasing frequencies up to 6.5 kHz.



13. Performance on an underwater audio-direction task as a function of auditory angle and sound frequency.



14. Performance on an underwater audio-direction task as a function of sound frequency.

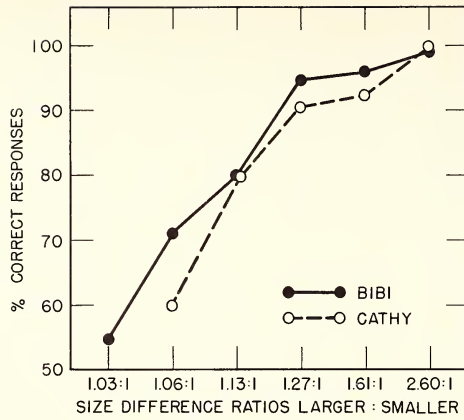
The data points at 1.5 kHz and 2.5 kHz do not differ significantly from chance. Apparently, even at an angle as wide as 25° , Zalophus cannot locate a sound at frequencies much below 3.5 kHz. The reason for this is not as yet clear, and obviously more data are needed. It may, however, be a function of a decreased sensitivity of Zalophus to low-frequency sounds or an unfavorable signal to noise ratio at the low end of the spectrum. Interestingly, Dudok van Heel (17) also found that the porpoise, Phocaena phocaena, was not proficient at localizing a 2 kHz tone.

The present data indicate that, under water, Zalophus and Phocaena have nearly the same degree of acuity of audio-direction at similar frequencies. At 6 kHz, the minimum auditory angle for the porpoise was 8° and for Zalophus it was 10° . At 3.5 kHz, the minimum angle increased for both species-- 12° for the porpoise and 15° for Zalophus. It may be concluded that the California sea lion is as capable as Phocaena in locating the direction of underwater sound.

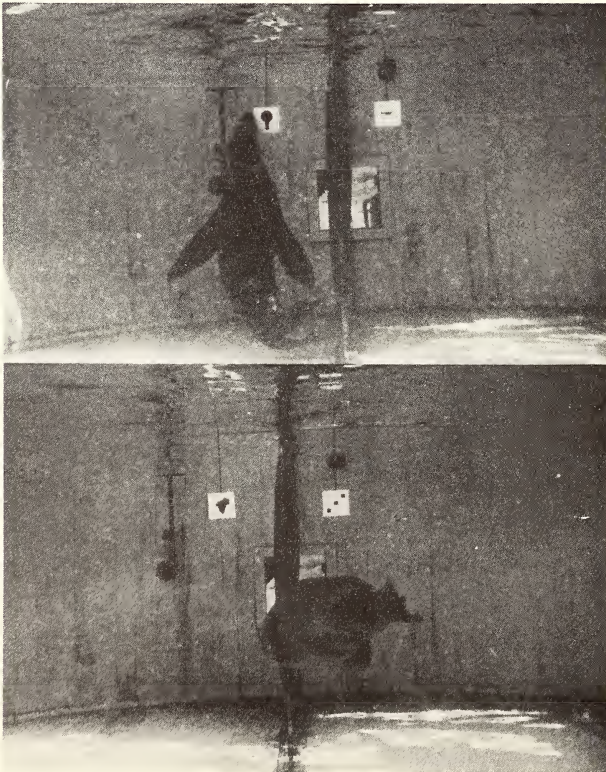
It should be noted that subsequent to the undertaking of these directional hearing experiments with Zalophus, we became aware of Møhl's (43) recent findings showing that under water the harbor seal (Phoca vitulina) can reliably locate the direction of a 2 kHz tone at 3.1° azimuth from the median plane.

V. Underwater Visual Perception

Anatomical evidence suggests that pinnipeds have compensated for the loss of the refractive power of the cornea under water by having a large spherical lens which produces enough accommodation to form a reasonably well-defined image on the retina (70). Recent behavioral data on the underwater size discrimination ability of two California sea lions have confirmed this anatomical evidence (62). Differential



15. Performance curves of two sea lions on a size-discrimination task.



16. A California sea lion (a) indicating its choice on a pattern discrimination task, and (b) swimming toward a new stimulus pattern display. Note the relatively low position of the animal.

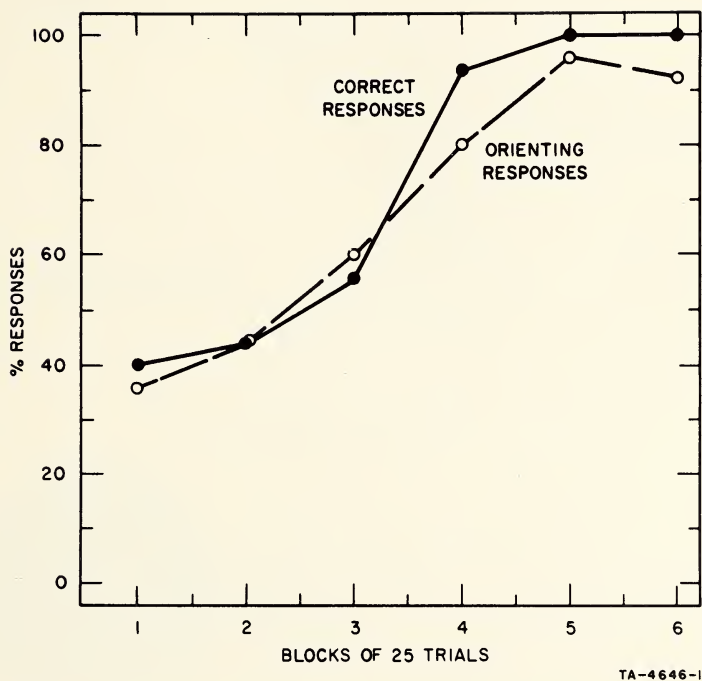
size-thresholds were obtained by the psychophysical method of constant stimuli. The two sea lions (Bibi and Cathy) were always required to respond to the smaller of two triangular or circular targets, and were forced to make a decision at least 1.2 m prior to giving an indicator response. Results of this experiment are presented in Fig. 15, which shows that as the magnitude of the size-difference ratios increased, there was a corresponding increase in correct responses. The figure also reveals that both animals were capable of discriminating a size-difference ratio as small as 1.06:1. Additional data with the Steller sea lion and the harbor seal indicate that these two species of pinnipeds are also capable of discriminating a size-difference ratio of about 1.06:1. If the discrimination of size-differences may be taken as a gross measure of visual acuity, then Zalophus and other species of Pinnipedia may be said to have good underwater visual acuity. Indeed, comparison of Zalophus' results with those of such "visual" animals as the Java monkey (35), and the squirrel monkey (63) reveals little difference in the size-discrimination ability of these divergent mammalian forms.

In addition, preliminary data (59) demonstrating accurate discriminations by Zalophus under darkened conditions (discriminations which could not be made in the same period of time by the human observer) combined with the anatomical evidence indicating the apparent nocturnal adaptations of the pupil, retina and choroid of the pinniped eye (70) suggest that in dim illumination the visual acuity of Zalophus may be superior to that of man. Furthermore, a recent study of underwater discrimination and transfer by the California sea lion revealed remarkably efficient discrimination of stimulus figures differing only with regard to shape (61). Most of these discriminations were maintained near or at a perfect level of accuracy even when positive, negative or both shapes underwent changes

in orientation of 45° , 90° or 180° . Moreover, some unpublished experiments by the author suggest that Zalophus may be capable of solving a wide range of visual discrimination problems of the types shown in fig. 16 after only a single information trial. In line with Hobson's (28) recent observations regarding the tendency of seals and sea lions to approach from below and silhouette their prey (fish) against the ambient surface light even at night, all animals tested thus far approached stimulus targets from a position considerably beneath the lower edge of the targets (see Fig. 16).

From data such as these, it may be expected that Zalophus and some other pinniped forms would rely strongly on visual cues for the detection and discrimination of underwater objects. Further evidence supporting this viewpoint was obtained in an experiment dealing with the gross orienting responses of Zalophus (58). Orienting responses were defined as postural changes of the head or body occurring within approximately 2 m of the stimulus display.

Following a demonstration of perfect discrimination in clear water between a large black circular disk (736.1 cm^2 in area) and a small black circular disk (16.1 cm^2 in area), sea lion Cathy was confronted with the identical discrimination task in turbid water. A harmless vegetable dye (see Schusterman, 1966) was poured into the water so that visibility was attenuated to a distance of approximately 2.8 m, i.e., the maximum distance at which a skin diver was capable of perceiving the larger target. Presumably the animal was unable to perceive the stimulus display when it began its approach approximately 6 m away. Following 150 training trials in turbid water, Cathy was tested alternately in clear water and turbid water. Figure 17 presents the effects of reduced underwater visibility on Cathy's performance. Even though the discrimination had been perfected prior to making the water turbid, and despite the fact



17. Acquisition of orienting and correct responses in turbid water.

that visibility under water had not prohibited discriminability in advance of the choice point (approximately 1.2 to 1.5 m), Cathy averaged less than 60% correct responses during the first 75 trials. As the figure clearly shows, the acquisition curve for correct responses is closely paralleled by the acquisition curve for orienting responses. This experiment was replicated with two other California sea lions with essentially the same results.

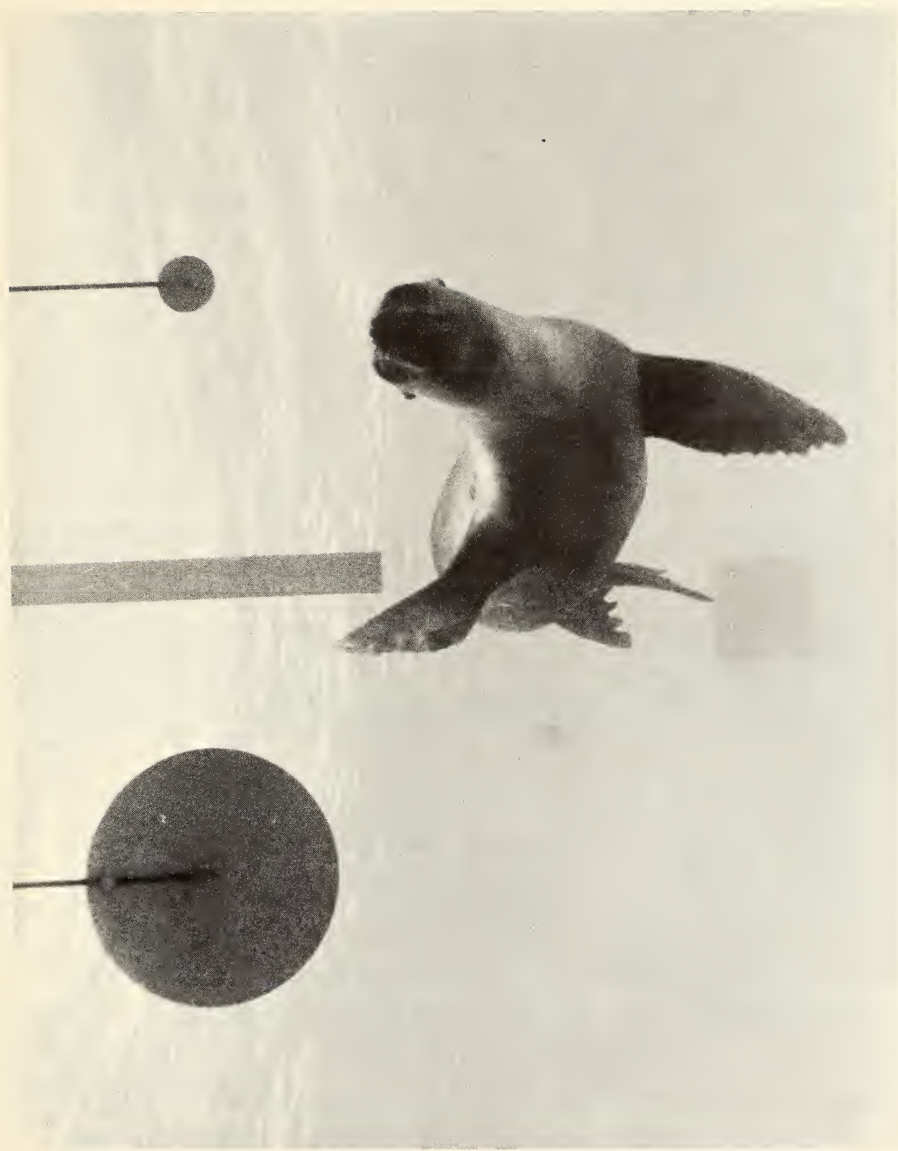
Thus, sea lions swimming in mildly turbid water--which completely occluded their vision as they began their approach toward a stimulus display--learned orienting responses of the head and body in order to discriminate visually between two target stimuli. Discrimination performance remained perfect in both clear and turbid water, but orienting responses remained highly probable only during the latter condition. These results suggest that sea lions rely primarily on postural adjustments and fixating responses of the head and eyes in order to discriminate effectively between two different size objects.

VI. Factors Influencing Production of Clicks and Other Underwater Vocalizations

A. Visibility

Previous exploratory studies have shown that when a captive California sea lion is confronted with an underwater discrimination task, permitting little visibility of the stimuli, it produces clicking sounds and tends to increase the amount of these vocalizations as a function of the degree of water turbidity (59).

Although these quantitative studies were carried out in the laboratory with a single animal, the results have been corroborated by observations on two other California sea lions in another laboratory setting and in the open sea (Evans, personal communication).



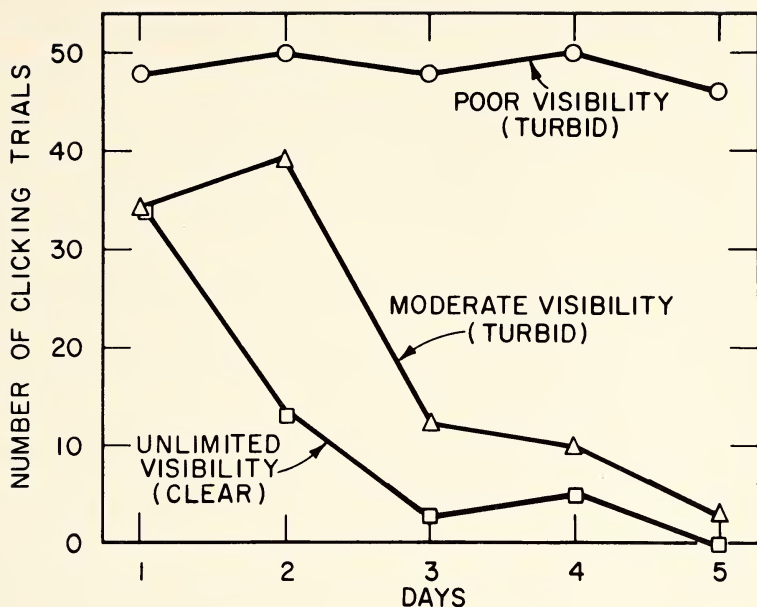
18. A sea lion approaching the smaller of two targets.

On the basis of these results, a hypothesis was formulated suggesting that in addition to being related to the animal's general arousal level, underwater clicking by the California sea lion may be an information-seeking response and thus may be one component of the orienting reflex in this particular species of pinniped.

Thus far, there has been no systematic attempt to vary the degree of underwater visibility over a relatively long period of time in order to determine the joint effect of trials and visibility on the probability of clicking. The following study was designed to do just that and was carried out until the frequency with which a sea lion produced a series of clicks reached asymptotic values under three conditions of visibility (clear water or unlimited visibility and maximum visibilities of 2.7 to 2.8 m and 0.74 to 0.81 m). Since sea lion Bibi had been clicking on virtually every trial under an extremely low visibility condition just prior to this experiment (59), it was hypothesized that the animal would continue its high level of clicking under similar conditions of the present experiment and demonstrate habituation of clicking following a relatively high probability of clicking during the initial trials of the clear-water condition.

Sea lions Bibi and Cathy participated in the experiment. Previously they had both received training on a size discrimination task in clear water and most recently had been tested in turbid water in attempts to demonstrate their "active sonar" capabilities (59). During the latter experiments Cathy received only a few hundred test trials without ever producing a vocalization of any kind, as compared to more than 2500 trials received by Bibi, who made clicking sounds during most of the trials.

Under all three visibility conditions, the animals were required to respond in accordance with their most recent training, Bibi to the larger of two targets and Cathy to the smaller (736.1 cm^2 - 16.1 cm^2 in area).



19. Underwater click vocalizations as a function of visibility conditions and test sessions or days. The ordinate shows the number of trials during which a sea lion produced a train of clicks.

Table 1

Response Latencies (in seconds) as a Function
of Visibility Conditions

Condition	Sea Lions			
	Bibi		Cathy	
	Median	Range	Median	Range
Unlimited visibility (clear)	2.9	2.2 - 3.8	3.0	2.1 - 4.2
2.7-2.8 meter visibility (turbid)	3.2	2.3 - 4.5	3.5	2.3 - 4.8
0.74-0.81 meter visibility (turbid)	3.9	2.9 - 5.4	4.5	3.2 - 5.8

The targets were black circles made of 20-gauge steel. Figure 18 shows the type of discrimination used in this study. For the two limited visibility conditions the water was made turbid by means of a vegetable dye. A standard sequence was used each day in a pre- and post-test design. The sequence on each of five consecutive days was as follows:

1. Pre-test. Twenty-five trials of unlimited visibility (clear water).
2. Moderate visibility. Fifty trials with a maximum visibility of from 2.7 to 2.8 m.
3. Poor visibility. Fifty trials with a maximum visibility of from 0.74 to 0.81 m.
4. Post-test. The tank was emptied and refilled with clear water, and the sea lions received 25 additional trials under the unlimited visibility condition.

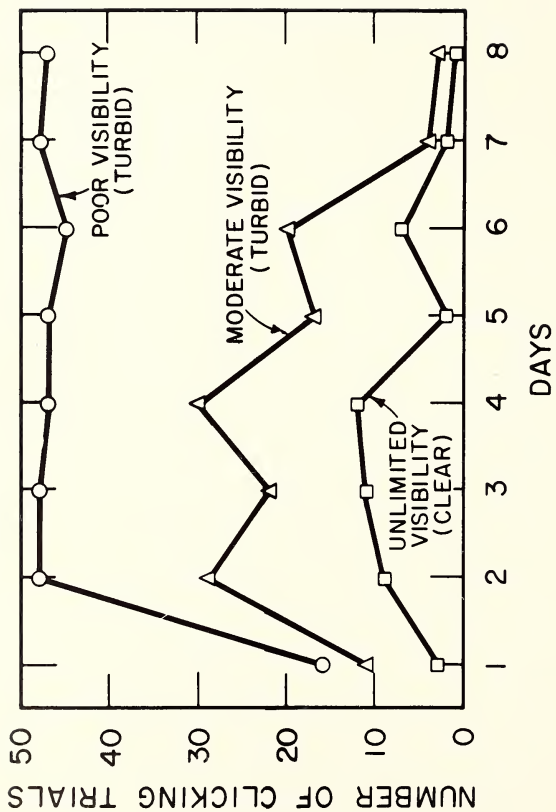
In order to minimize the use of visual cues under the poorest condition of visibility, an earlier series of exploratory studies suggested the use of a 1.2-m divider or barrier (extending outward between the target stimuli) and a procedure whereby an incorrect response could be scored when an animal's nose was just past the side of the barrier on which the incorrect target was located. Since the maximum visibility under the most turbid water condition was considerably less than the distance that the barrier extended outward between the targets, it was assumed that the animals had to make a decision prior to giving the indicator response (pressing the target) at a distance from the stimulus display which afforded virtually no visual information.

Results. There was no difference in the pre- and post-tests; therefore, these results were combined into one condition (unlimited visibility). The main results are presented in Fig. 19. Since Cathy remained silent

throughout the entire experiment, results of this animal are not represented in the figure, which shows that the frequency with which Bibi made clicking vocalizations varied as a joint function of the visibility conditions and the length of time it experienced each of the conditions. As expected, although both animals made almost no errors under the unlimited and moderately limited visibility conditions, they performed near chance when visibility was very poor.

Both sea lions frequently displayed orienting responses of the head or body within 2 m of the stimulus display under both turbid water conditions, but rarely showed such activity in clear water. This behavior is reflected in the response latencies of both animals as shown in Table 1. Predictably, on the basis of the ease of target discriminability, response latency increased as visibility decreased. Latency scores within each of the conditions showed only minor fluctuation from session to session. It should be noted that response latencies for the poorest visibility treatment were based on correct-response and not incorrect-response trials, since targets were usually withdrawn from the water as soon as an animal passed the barrier on the side of the negative target.

Discussion. Although Cathy proved to be a nonvocal animal in each underwater discrimination task, regardless of the degree of visibility, the frequency with which Bibi made clicking vocalizations as a function of visibility was shown to depend upon the length of time this sea lion experienced each of the visibility conditions. Thus, Bibi's results confirmed the initial hypothesis that although underwater clicking during a discrimination task may persist under a continuing state of impoverished visual information, the vocalizations have a higher probability of occurrence during the initial stages of unlimited visibility, habituating at a negatively accelerated rate until there is virtually no clicking at all. Conditioning could not have been a factor since reinforcement was more

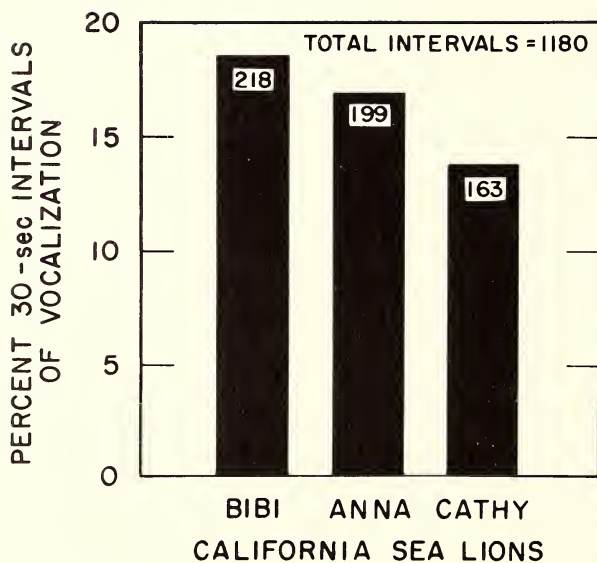


20. Underwater click vocalizations under three conditions of visibility following habituation of clicks in clear water.

probable under conditions of unlimited visibility than under conditions of poor visibility.

Of particular interest was the unpredicted finding that, although the early stages of testing resulted in a higher probability of clicking in moderately turbid water than in clear water, the decline in clicking was more rapid in the former condition, so that the curves describing the clicking probability functions for the two conditions eventually converge at a value near zero.

Since the target stimuli were invisible when an animal began its approach in mildly turbid water, but became visible well in advance of the choice point, it seems likely that the sea lion gradually learned to anticipate target discriminability under this condition. On the basis of this assumption, this animal's results suggest that underwater clicking, rather than being directly related to the turbidity of water as such, depends upon the degree of certainty with which a sea lion can make a decision at the choice point prior to its giving an indicator response. Thus, a clicking vocalization as one aspect of information-seeking behavior does not habituate under conditions of uncertainty which induce and maintain a constant state of conflict and arousal (poor visibility condition), but does habituate under conditions offering little uncertainty. This is so either because the animal can readily distinguish between the food-signalling-stimulus and the nonfood-signalling-stimulus and thus respond appropriately (unlimited visibility condition) or because, by gradually learning, the animal comes to anticipate eventual signal detectability and discriminability prior to making an indicator response (moderate visibility condition). Such an interpretation is consistent with Berlyne's (9) notions relating the influence of conflict induction to the arousal properties of the organism and concomitant information-seeking behavior. Furthermore, if underwater clicking by



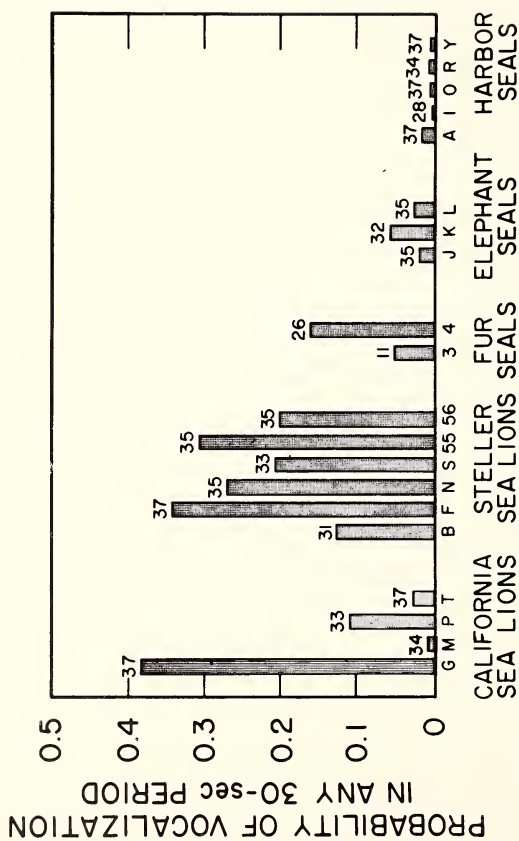
21. Percentage of 30-sec.intervals in which three females emitted any type of airborne vocalization. The number of intervals in which an animal vocalized appears at the top of each column.

Zalophus is in fact one aspect of an orienting reaction, then the persistence of such a reaction is not unexpected. For example, Berlyne, in summarizing the Russian work relating properties of the orienting reflex to stimuli with signal value, states that "the orienting reaction will be singularly intense and last more or less indefinitely if a stimulus with signal value is hard to detect, e.g., because it is near the absolute threshold." (9, p.88).

Although the data from one animal, Bibi, are quite reliable, the fact that Cathy produced no clicking vocalizations under nearly identical conditions discourages any broad generalizations deriving from these results. However, in order to check the reliability of these data even further, a second similar experiment was performed with Bibi. Prior to the initiation of the experiment proper, the animal received approximately 400 trials on a simple size discrimination in clear water and remained relatively silent during each of the trials. On the basis of the previous results and the suggestions formulated from those results, it was predicted that the likelihood of clicking would remain low in clear water, increase to a probability of close to 1.00 under conditions of poor visibility, and increase to some moderate value and then decline to a near-zero value under conditions of moderate visibility. As Fig. 20 shows, the predictions were confirmed. Again, performance in terms of correct responses was perfect in clear water and near chance when visibility was poor.

B. Degree of Airborne Vocalization

The individual differences of the last experiment raise an interesting question concerning the relationship of clicking under water to the general vocalness of a sea lion in air. As a result of general observations made during the course of maintaining three California sea lions (including the two used in the last experiment), it was noted that Cathy appeared to



22. The degree of airborne vocalizations emitted by 20 seals and sea lions. The number of observation sessions for each animal appears at the top of each column.

Table 2

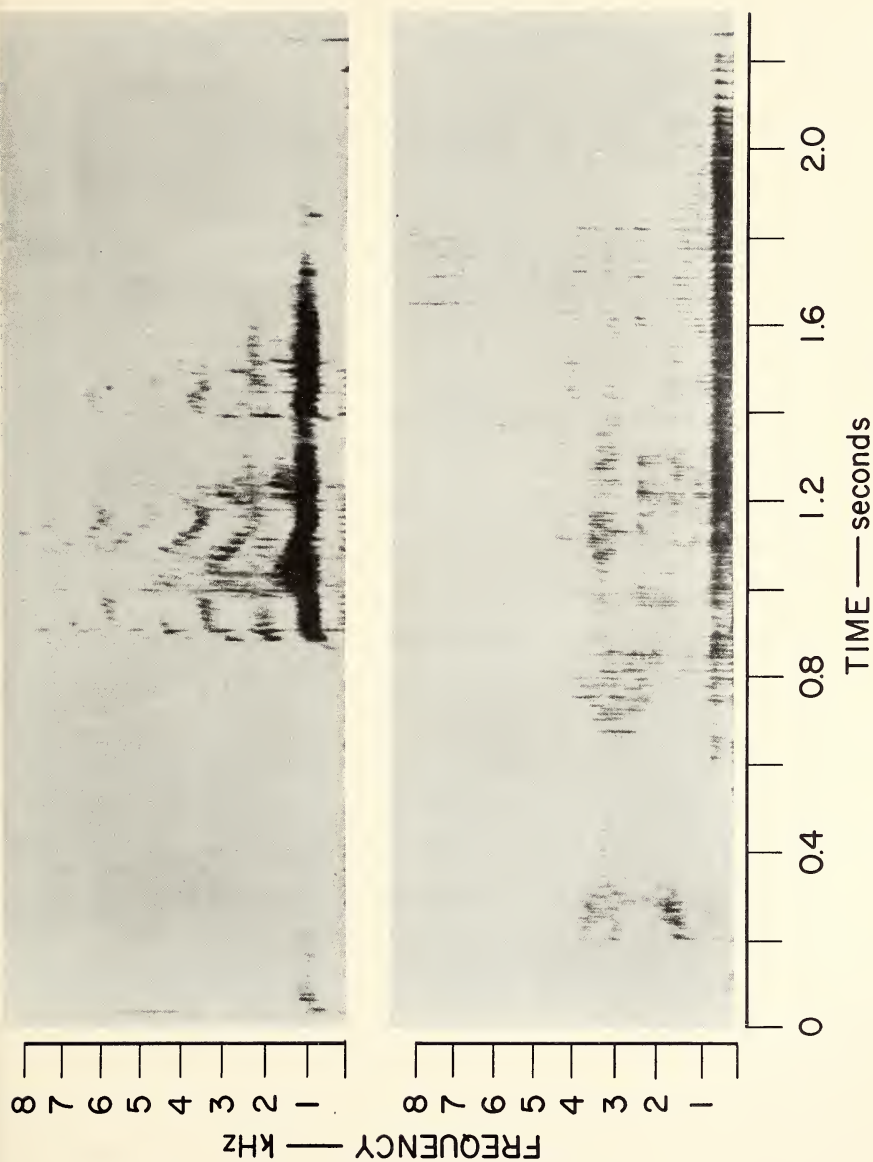
<u>Characteristics of Seals and Sea Lions used in the Vocalization Survey</u>					1.
Animal	Species	Sex	Approximate Age (at time of survey)	Capture Age	
G	<u>Zalophus californianus</u> (California Sea Lion)	M	4.5 yr.	3.5 yr.	2.
M	"	M	4.5 yr.	3.0 yr.	3.
P	"	M	1.5 yr.	1.0 yr.	
T	"	M	1.5 yr.	1.0 yr.	4.
B	<u>Eumetopias jubatus</u> (Steller Sea Lion)	M	1.5 yr.	< 1 mo.	
F	"	M	1.5 yr.	< 1 mo.	5.
N	"	M	1.5 yr.	< 1 mo.	
S	"	F	1.5 yr.	< 1 mo.	6.
55	"	M	5 mo.	< 1 mo.	
56	"	F	5 mo.	< 1 mo.	
3	<u>Callorhinus ursinus</u> (Northern Fur Seal)	M	3 mo.	< 1 mo.	7.
4	"	M	3 mo.	< 1 mo.	
J	<u>Mirounga angustirostris</u> (Northern Elephant Seal)	M	1.0 yr.	1 mo.	8.
K	"	M	1.0 yr.	1 mo.	
L	"	F	1.0 yr.	1 mo.	
A	<u>Phoca vitulina</u> (Harbor Seal)	F	Adult	Adult	9.
1	"	F	7 mo.	1 day	
O	"	M	1.5 yr.	1 mo.	10.
R	"	F	1.5 yr.	1 wk.	
Y	"	F	1.5 yr.	< 1 mo.	11.

be the least vocally responsive animal of the group. This observation offered the obvious suggestion that Cathy's threshold for underwater click vocalizations may have been considerably higher than that for Bibi. Fortunately, a check on this suggestion was available in the form of previously collected data dealing with the social behavior of three captive California sea lions. Behaviors, including virtually all vocalizations, were recorded by 30-sec. intervals on a time-ruled check sheet from May to August, 1964. The data dealing with the vocalizations are presented in Fig. 22; they support the suggestion that Cathy's low level of vocalization in air may have been partly responsible for its previous lack of underwater clicking.

If the degree of sound production in pinnipeds is similar both in air and under water, then an estimate of in-air calling may be helpful in predicting whether one or another species will be more or less vocal under water. Therefore, a preliminary survey of the in-air vocalizations of 20 seals and sea lions, representing five species of Pinnipedia was undertaken in November, 1965 and lasted approximately five weeks. The characteristics of the animals used in the survey are listed in Table 2.

The animals lived together in a large compound with a pool and were usually fed prior to the observation sessions, which took place twice daily--at 1:30 P.M. and 4:30 P.M. Vocalizations were recorded at 30-sec. intervals on a time-ruled check sheet. Vocalization of any sort was scored only once during a 30-sec. period. Each observation session lasted 10 minutes.

The results are presented in Fig. 22. From these data, it would be predicted that both the Steller and California sea lions would be considerably more vocal under water than would the harbor seal with the northern elephant seal occupying an intermediate position. Barking was the dominant vocalization of the California sea lion and clicking and hissing the



23. (a) Sonogram of an airborne "distress" cry from a captive one-month-old northern elephant seal (wide band). (b) Sonogram of an airborne "belch-roar" from a captive yearling northern elephant seal (wide band).

the dominant vocalization of the Steller. The harbor seals were relatively silent; their predominant vocalization being a growl, sometimes followed by a pulsed snorting sound from the nose. This sound is typically used in the harbor seal threat pattern. There were two distinct types of elephant seal calls. The predominant one was a shrill "distress" cry, sometimes with a hodeling quality which is typical of pups in the wild as described by Bartholomew and Collias (8). A highly pulsed call began to emerge in early December, 1965 which was similar to the "belch-roar" of the yearling as described by Bartholomew and Collias (8). Sonograms of these two calls are shown in Fig. 23. It is probable that the distress cry was yielding to the belch-roar as the pups reached yearling status. Since these animals had been in the presence of yearlings and adult elephant seals only for a brief time after birth (about one month) and since that time had been in the company of California and Steller sea lions as well as harbor seals, it is unlikely that the acquisition of the belch-roar was learned. Rather, the evidence suggests that the development of this vocalization is genetically acquired.

C. Conflict and Frustration

An organism is said to be in conflict when two or more incompatible response tendencies are aroused simultaneously (9). Frustration is often a consequence of conflict since the conflicting response tendencies may be a factor in blocking the organism from acquiring an incentive or goal object such as food. In previous experiments, it was indicated that underwater clicking may be evoked as a component of the orientation reflex by a stimulus situation which is relevant to conflict and/or frustration. Evidence supporting this point of view is now presented with a second California sea lion (Sam, a 3-year-old male). Since some of the procedural details of this experiment are not relevant to the present discourse and in fact have been partially presented elsewhere (61), only pertinent

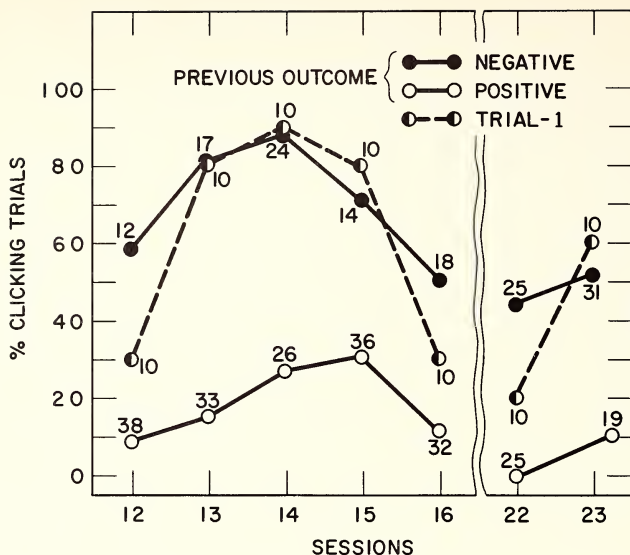
aspects of the procedure will be dealt with here.

In this study, the animal was presented with all possible two-choice discrimination problems which could be generated from 20 stimulus shapes. Since there are 190 combinations of 20 stimuli taken two at a time, and since each combination yields two problems (by reversing polarity of reward), a total of 380 distinct problems were constructed. Generally the animal received 10 different problems lasting 6 trials each for a total of 60 trials at a given test session. Thus, the animal had no information as to which stimulus shape would pay off on the first trial of each problem. However, following the initial trial of a problem, reward was consistently associated with one or the other of the stimulus shapes for the next 5 trials.

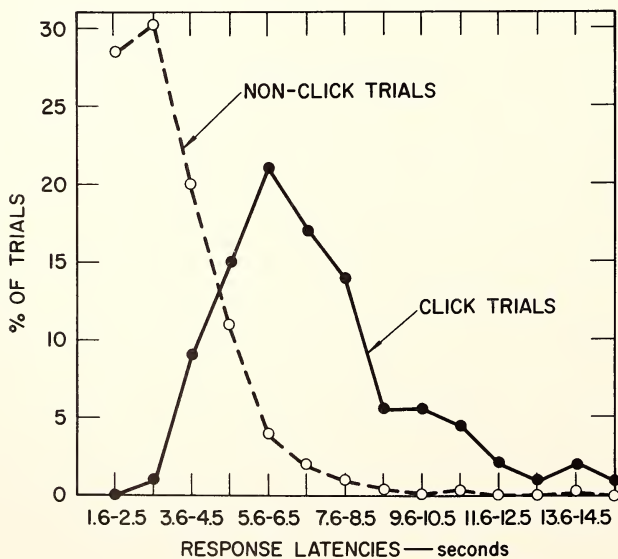
The sea lion produced no clicks during the early problems. However, by the sixteenth session, a few clicks were produced. On a typical "clicking" trial, the animal would swim to the choice point, turn its head and body to one and then the other stimulus, swim just below one of the stimuli and begin emitting a train of clicks. The clicks terminated as the animal indicated its choice by pressing against the stimulus target. As the study progressed, three principal features developed:

1. Clicking was acquired, lost, reacquired, and lost again with reinforcement of correct responses (to one stimulus shape or another) having little effect on click production.

2. During those test sessions in which click trains were produced quite frequently (sessions 12-16 and 22-23), occurrence could be readily predicted from trial to trial. Clicks were usually elicited either on the first trial of a new problem (trial-1) or on a trial following a previously incorrect or nonreinforced trial (negative outcome). On the other hand, clicking occurred relatively infrequently on a trial following a correct or reinforced response (positive outcome). Figure 24 illustrates



24. Percentage of clicking trials as a function reinforcement (positive outcome), nonreinforcement (negative outcome) and the first trial (trial-1) of each shape discrimination problem. The ordinate shows the percentage of trials during which a sea lion produced trains of clicks. Numerals at each data point refer to number of trials.



25. Distribution of response latencies as a function of "click" or "nonclick" trials.

this point by showing clicking as a function of previous outcome and trial-1.

3. Response latency or reaction time, i.e., the time between when the stimulus display was submerged until the time the sea lion pushed the target with its nose, was considerably longer on those trials when the animal vocalized than when it remained silent. Figure 25 illustrates this point by showing the distribution of response latencies as a function of "click" and "nonclick" trials.

The psychological literature is replete with demonstrations showing that reaction time is increased when an organism is in a state of conflict and that nonreinforced responding leads to frustration effects. Thus, in the present context, when the animal was reinforced, it would appear that conflict and frustration were somewhat reduced, resulting in more rapid responding without click emission. If, however, the animal was confronted by a new problem or had made an error on the previous trial, then it was much more hesitant in its final choice response, and just prior to its choice, it often emitted clicks.

This evidence tends to support the hypothesis that elicitation of clicks in turbid water may not be a function of reduced visibility as such, but rather a function of the stimulus situation which induces an organismic state of conflict and arousal.

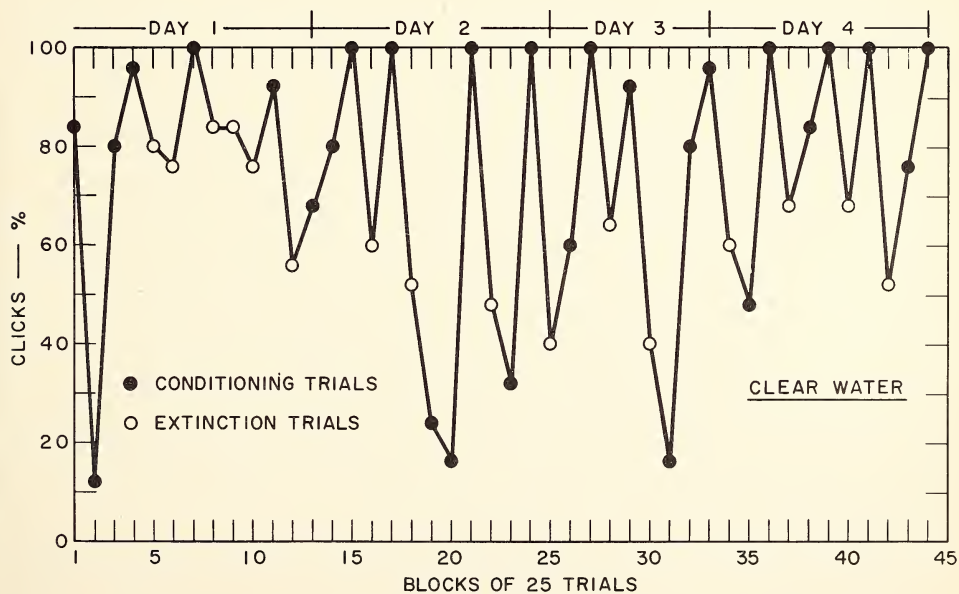
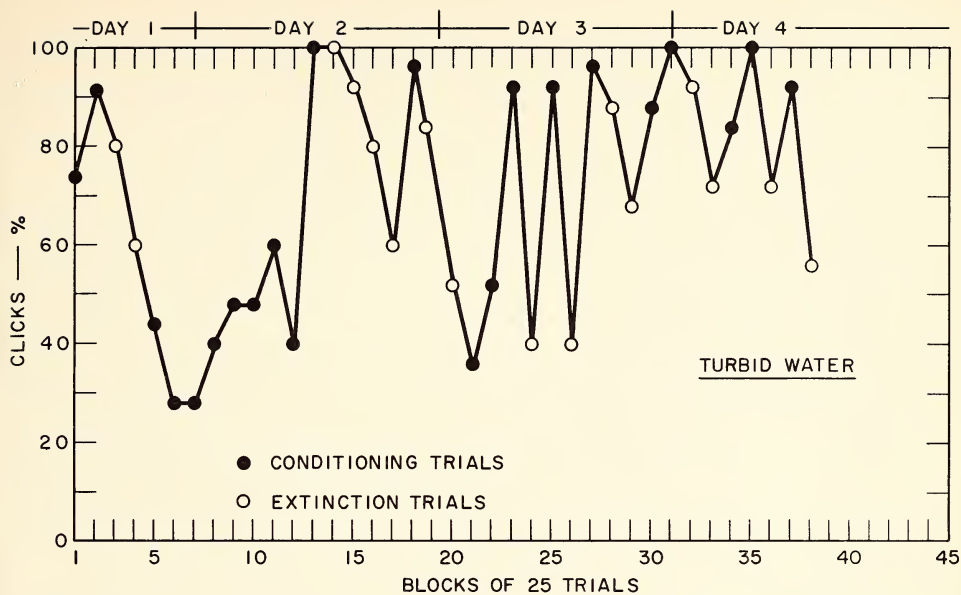
D. Operant Conditioning

A response by an animal, e.g., a pigeon raising its head to a certain height, may be conditioned as a result of its consistently being followed by the occurrence of a reinforcing event such as food. This type of conditioning has been called operant conditioning as distinguished from classical or Pavlovian conditioning (64). If a sea lion is maintained for a relatively long time in an aroused or alert state in which click vocalizations are invariably evoked (such as when it is confronted with

a difficult detection or discrimination task), then any food reinforcement which immediately follows may inadvertently result in the conditioning of such vocalizations. On the other hand, it has been suggested that since most known nonhuman animal vocalizations are elicited by unconditioned stimuli, it is difficult, if not impossible, to control them by such operant conditioning procedures (65,67).

Studies with rats, showing that squeaking could be controlled by classical but not by operant or instrumental conditioning procedures (cf.46) tend to support this view. Recently, however, operant conditioning procedures have proved successful in modifying vocalizations by a variety of mammalian forms. Included are the dog's bark (54), the cat's meow (45), the porpoise's squawk (39), and the young cebus monkey's musical "Ooo" (44). Therefore, the question arises as to whether a clicking vocalization by a sea lion could be controlled or conditioned by means of operant reinforcement techniques in both clear and turbid water. This question was subjected to experimental analysis.

Using a counter-conditioning paradigm, fish reinforcement was made contingent on either clicking or not clicking, depending upon whether the acquisition or extinction phase of the experiment was in progress. Each trial was initiated by presentation of two identical target stimuli which were used only as an approach signal. Since previous explorations suggested that it would be inefficient to extinguish clicking completely, the criterion for the acquisition of clicking was more rigorous than that for inhibiting the output of clicking sounds. During acquisition or conditioning, the sea lion (Bibi) was required to emit a series of clicks on 23 trials of a block of 25 trials taken as an independent unit. During extinction of clicking (or acquisition of nonclicking) the animal was required to inhibit its clicking vocalization on 6 of 25 trials. Following



26. Successive acquisition and extinction of underwater click vocalizations by a California sea lion.

a successive acquisition and extinction series in turbid water (visibility as measured by a skin diver was approximately 2.7 to 2.8 m), the series was replicated in clear water.

On a typical trial, when the two targets were presented Bibi would dive under water and begin a train of clicks about 2.4 m from the stimulus display area. Initially clicking would terminate just prior to touching one or the other of the targets. However, by the third day of turbid-water testing, the animal often continued to emit clicks even after pushing a target. Even though food reinforcement was contingent only upon a vocal response or the inhibition of a vocal response, the animal went through three different phases of systematic responding to target position. Initially the animal alternated position; then it persevered to either position, and finally it consistently pressed against the target on the left. At first, targets were pushed vigorously; however, about half-way through the experiment responses to the target were perfunctory, with the animal barely touching it.

The curves for both the clear and turbid water phases of the experiment are presented in Fig. 26. The figure shows that the California sea lion's underwater click emission is subject to control by operant conditioning techniques. Since Bibi had been producing trains of clicks in turbid water just prior to the present study (see Section VI, A) the initially rapid acquisition of clicking on Day 1 was not unexpected. Following the first extinction session, reacquisition proceeded more slowly and Bibi had to be given 200 trials before reaching the criterion for acquisition. However, by the third day, reacquisition of clicking usually occurred soon after the first click trains were emitted and reinforced.

Thus, repetition of acquisition and extinction sessions resulted in a progressively more rapid transition between high and low degrees of this

vocal behavior. This phenomenon has been demonstrated in simple lever-pushing situations (13) as well as in more complex discrimination problem-solving situations (27) and has sometimes been called "learning set" or "learning how to learn." Since there was no exteroceptive cue correlated with the beginning of the conditioning or extinction periods, the discriminative control of vocal behavior must have been a function of cues associated with reinforcement and nonreinforcement. If, as has been suggested by Salzinger and Waller (54) and others (29), the vocal behavior of animals constitutes an evolutionary forerunner of human verbal behavior, then it seems likely that the phenomenon of learning set formation will also be found in the development of human verbal behavior.

As already indicated, there is some evidence to suggest that the production of underwater clicking sounds may be related to the general vocalness of a sea lion. Further support for this notion occurred when Bibi and Cathy were placed together in the experimental tank and were trained to make an instrumental response (each striking simultaneously presented targets of different size) for food reinforcement. Both animals were highly aroused, as evidenced by their raucous play and aggressiveness between trials, but Bibi alone produced barks and clicks. On this basis, it was proposed to condition Cathy to vocalize in air and to determine whether, in its attempt to vocalize under water, the animal would begin to emit clicking sounds. Accordingly, a series of experiments was initiated with the aim of shaping an underwater clicking vocalization by Cathy and then gaining discriminative control over the vocalization (60).

Conditioning of Cathy's airborne vocalizations was extremely rapid and was accomplished by holding a piece of fish in front of the animal

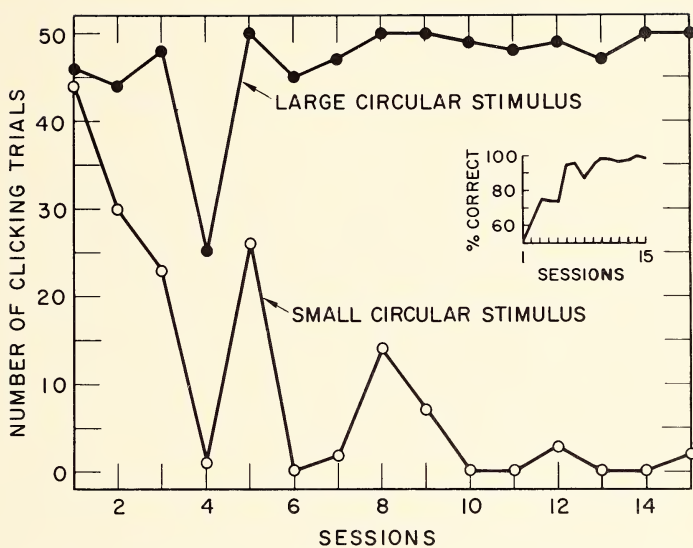
until it vocalized. Each vocalization was promptly reinforced with a piece of fish. Next, the animal was placed in the tank and had to duck its head under water and vocalize prior to target presentation and subsequent food reinforcement. An initial click train occurred within the first 5 minutes and the animal acquired consistent click emission within approximately 30 minutes. Finally, discriminative control over Cathy's underwater clicking vocalization was demonstrated.

Using a counter-conditioning paradigm, a clicking vocalization in the presence of a large (736.1 cm^2) circular target was reinforced, and not clicking in the presence of a small (16.1 cm^2) circular target (the one that the animal had originally been trained with) was reinforced. The targets were presented successively in a random sequence within blocks of 100 trials; each was presented on 50 occasions at each test session. There were two test sessions on each of the first three days, and thereafter one test per day. Figure 27 presents the results of this experiment, and shows that virtually complete discriminative control over Cathy's underwater clicking was accomplished within three days, after 600 trials.

If the underwater clicks produced by Zalophus are part of an active biological sonar system, then these results suggest that at least the first stage of the system, i.e., the emission of short duration sound pulses, is highly flexible and subject to external modification.

E. Social Interaction and Novelty

Vocalization often appears related to alertness or a relatively high activity level of an animal and it may be assumed that during such activated states a high degree of physiological arousal exists (10,18). Among sea lions in captivity and in nature, vocal displays in air (sounds which often have a pulsed structure) have considerable communicative



27. Acquiring and maintaining discriminative control of underwater click vocalizations. The sea lion was reinforced for clicking in the presence of a large circular stimulus and for not clicking in the presence of a small circular stimulus. Insert shows acquisition of correct indicator responses (vocalizing or not vocalizing).

value and are frequently associated with conditions of stress, social play, fighting or sparring, increased sexual activity, and disturbance from a resting state. It has previously been suggested (59) that underwater click vocalizations by the sea lion, Zalophus californianus, may be related to a general arousal phenomenon (9,10) as well as a specific or focused arousal such as the "questioning reaction" or "orienting reflex" (49,66). Since click vocalizations are likely to convey information concerning the moods of the vocalizing animal, these sounds also may function as a part of the underwater communication system of the California sea lion.

Novelty or stimulus change is a strong impetus to behavioral and physiological arousal, and the concept of arousal has recently been found useful in interpreting investigative behavior (72) as well as patterns of social behavior (42). If clicking vocalizations under water are related to the emotional character of Zalophus, then these vocalizations would be expected to play a prominent role in the animal's behavior in situations that on face value might be considered arousal-producing. To test this hypothesis, three sea lions were presented with a social stimulus (another sea lion) and two novel or strange stimuli (a large clown-like object, and a mirror) in a pre- and post-test experimental design.

The amount and types of underwater vocalizations were, in most cases, compared when the stimulus conditions were and were not present. Quantification of underwater vocal behavior and investigative behavior was accomplished by means of a time-ruled check list. Frequency of occurrence was recorded by 30-sec intervals. Thus, it was possible to obtain a minute-by-minute record of vocalization and object-investigation. Two Es observed the animals from the testing platform. One E monitored and scored the occurrence of underwater vocalizations, while the other E observed the

animals, using a stop-watch to record time only when an animal's head was submerged, scoring behavioral categories and making qualitative notes on the behavior of each animal. Vocalizations were scored only during "running time", i.e., when at least one animal had its head under water.

The animals used in these studies were a male (Sam) and two female (Bibi and Cathy) California sea lions, between 2 and 3 yr. old; all had been in captivity for at least 1 to 2 yr. Previously, Bibi and Sam had spontaneously produced underwater clicking sounds in different types of visual discrimination tasks (see Sections VI, A and B) and Cathy had been conditioned to emit these sounds (60).

Social. In this experiment, each of the three animals was paired with each of the other two on separate occasions. One pair was tested each day between 9:30 A.M. and 1:00 P.M. All three pairs initially received a total of four test sessions with one animal of each pair alternately introduced into the tank individually or as a "partner" (see below).

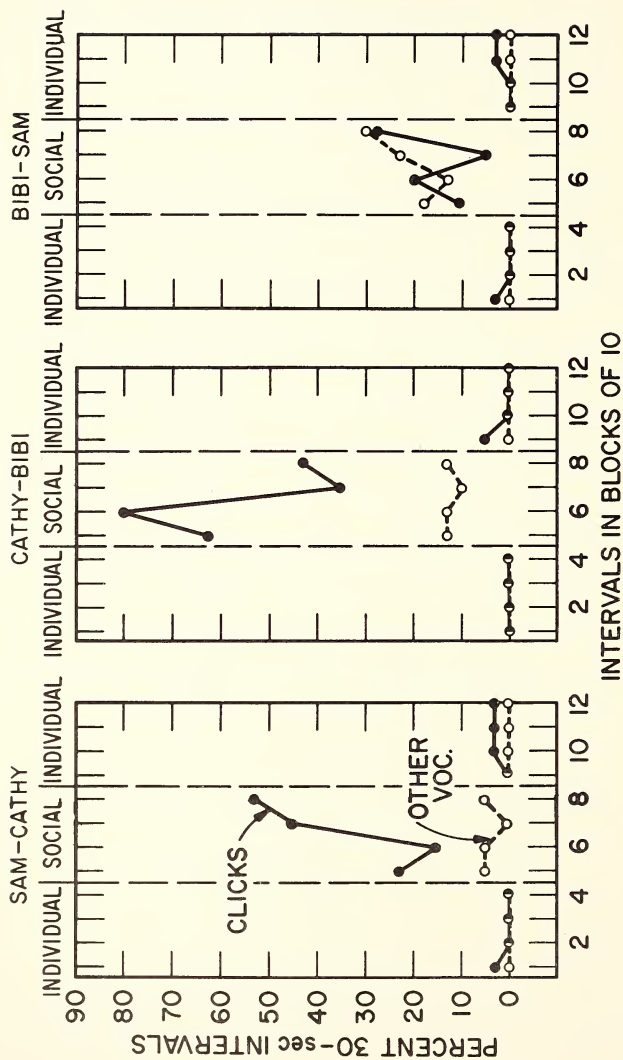
The procedure at any given session was as follows:

1. Adaptation. An animal was introduced into the tank and swam freely for one hour. Observations were made during the first 10 min. of this period.

2. Pretest or individual test. E recorded the underwater vocalizations of the single free-swimming animal for 20 min.

3. Social test. A second animal, the "partner", was introduced into the tank and underwater vocalizations by both animals were recorded for 20 min.

4. Post-test or individual test. The partner was removed from the tank and recording of underwater vocalizations by the first animal was resumed.

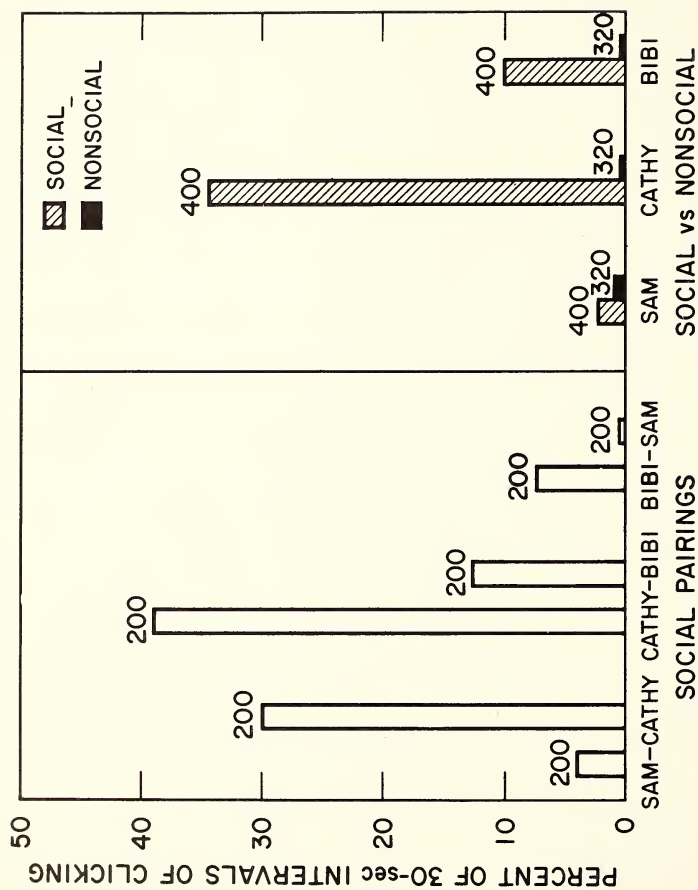


28. Degree of clicking and other underwater vocalizations when sea lions are tested individually and in pairs (social).

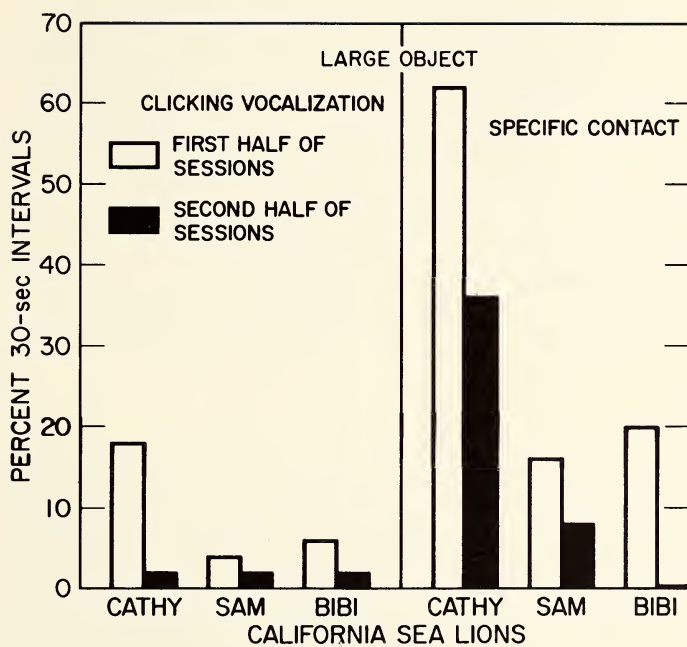
One session was run each day for 12 days.

The underwater vocalizations involved during this experiment included "whinny" sounds, barks, and a buzzing sound, as well as varying patterns of click trains. These sounds are displayed in the sonograms shown in figs. 3 to 9. Since there was little change in the amount or type of vocalization for each pair over the four test sessions, the results from each of the sessions were combined and are presented in Fig. 28. The degree of clicking and other vocalizations is expressed as percent of 30-sec.intervals. It is evident from the figure that clicks and other vocalizations were far more prevalent for each of the pairs during social testing than during individual pre- and post-tests. In fact, virtually no vocalizations occurred when the animals were tested alone. Note that the most vocal pair (Cathy - Bibi) produced click trains during more than 50 percent of the observation periods.

Since vocalizations frequently occurred when only one animal of a pair had its head under water, it was often possible to identify which one of a pair emitted the sound. Moreover, the pattern of click trains was usually highly distinctive for each animal, which further enabled identification of the sound-producing animal. The degree of clicking contributed by the individual sea lions during social interactions is presented in Fig. 29. This figure includes an additional (fifth) test session for each pair which was run without pre- and post-tests, and is not included in the summarized data of Fig. 28. The left panel of Fig. 29 shows the percentage of 30-sec.intervals in which individuals produced clicks in a given social pairing. These data show that although Bibi and Cathy produced clicks more frequently when paired with each other or with Sam than when solitary, Sam's production of clicks increased in a social situation only when paired with Cathy.



29. Degree of clicking contributed by individual sea lions in different social pairings and as a function of social and nonsocial conditions.



30. Effects of a large "novel" object on underwater clicking and degree of specific contact with the object. The figure compares the effects during first and last ten 30-sec.intervals.

Clicking was the predominant vocalization by all animals. However, Bibi frequently produced a "whinny" sound, especially when interacting with Sam. This vocalization was never emitted by the other two animals. Play-fighting was the most frequent social activity observed, and was characterized by chasing, gentle biting and pushing, and "porpoising" together and over one another. Although clicking was frequently in evidence during a social encounter, especially during an extensive chase, it occurred equally as often when the animals were not swimming in proximity to one another. On the other hand, barking and Bibi's "whinny" sound were specific to social encounters and usually occurred when play appeared to shift to aggression (consisting of hard biting and lunging).

The two most vocal sea lions (Bibi and Cathy) were also the most generally responsive. Cathy, in particular, appeared to be soliciting play from another animal by gently biting its rear flipper and following this with porpoising and rapid swimming over, under, and around the animal.

Novelty - 1 (large object). This first study dealing with the effects of novelty on underwater clicking was initiated as soon as the social experiment had terminated. The procedure and method of scoring were similar to those of the previous experiment except that the pre- and post-test design was not used. A large plastic clown, 127 cm high, with a maximum diameter of 51 cm, was weighted with water so that it could not readily float and was placed near the center of the tank. Each animal was introduced individually into the tank with the object and received five such test sessions (one per day). Each session lasted 10 min.

The combined results from the five test sessions are presented in Fig. 30 which compares the degree of clicking and specific object-contact by each animal during the first and last ten 30-sec. intervals. Although there was little change in either of these behavioral indices

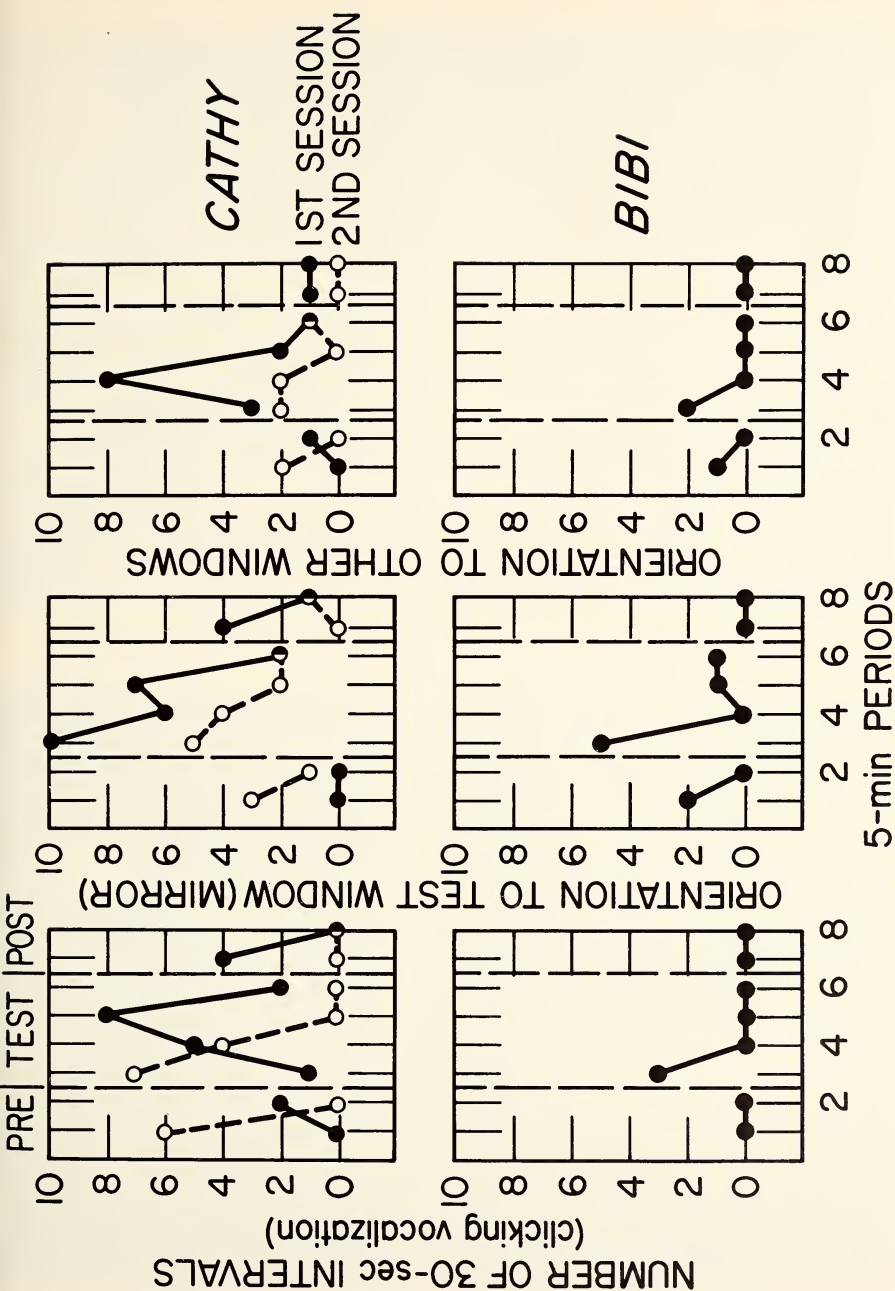


31. A sea lion biting and carrying the large plastic object.

over sessions, all animals showed either some decrease or no change in both measures within each of the sessions. Thus, there was a direct relationship between the degree to which an animal interacted with the object and the degree to which click vocalizations were elicited. However, the degree of clicking by Sam and Bibi was relatively low, preventing meaningful comparisons between the first and last halves of the sessions.

All animals contacted the novel object within the first min. of exposure. This initial contact was invariably made with the nose and repeatedly occurred during the first one or two min. of each of the succeeding sessions. Cathy was the only animal who manipulated the object by means other than just nuzzling (see Fig. 31). This sea lion showed great interest in the object and its repertoire of manipulations included pushing with the nose, biting and shaking, dragging the object with the mouth, and occasionally clasping it with its front flippers. The object was so mangled by Cathy's rough biting and "handling" that by the third session, the original object had to be replaced. Although clicking vocalizations occurred occasionally while the animals looked at the object, they occurred more often when an animal appeared to be paying little attention to the object.

Novelty - 2 (mirror). The following experiments sought to determine the effects of a mirror stimulus on the underwater vocal and investigative behavior of the sea lion. A mirror may be thought of as a novel stimulus, which to a certain extent has the properties of a social stimulus. Köhler (36) has shown that reflected self-images from a mirror or from pools of water elicit intense interest and investigation from chimpanzees, and Tinbergen (68) reports that a sexually active male stickleback will assume a threat posture upon seeing itself in a mirror.



32. The effects of a mirror stimulus on clicking and visual orientation during successive observation periods.

In the first experiment, a 41 x 51 cm mirror was hung outside the tank against the 51 x 51 cm window at the far end of the tank. The other five windows of the tank remained uncovered. In addition to scoring vocalizations, visual orientation to the test window (with the mirror) and to each of the other windows (except the one directly below the observation or testing platform) was also scored. Orientation was recorded when an animal looked at a window for at least 3 sec. within a distance of at least 0.9 to 1.2 m.

The procedure at a given test session was as follows:

1. Pretest. E recorded the underwater vocal and orientation behavior of a free-swimming animal for 10 min.
2. Test. Following removal of the animal from the tank and placement of the mirror outside the window at the far end of the pool, the animal was reintroduced into the tank and E tapped at the test window until the animal gave one orienting response. Scoring began subsequent to a sea lion's initial orientation to the test window and lasted for 20 min.
3. Post-test. While the animal was taken out of the tank, the mirror was removed from the test window. The animal was then reintroduced into the tank and recording was resumed as in the pretest.

One session was run on each of two consecutive days.

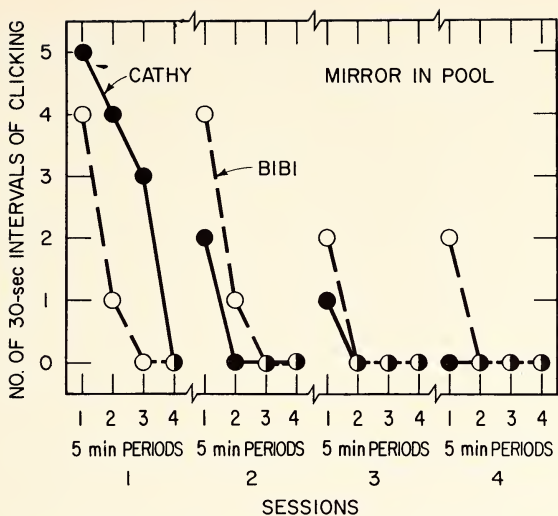
Repeated attempts to elicit orientation to the mirror from sea lion Sam failed and this animal was dropped from any further experimental analysis. In contrast, both Cathy and Bibi showed immediate orientation to the mirror; their results are shown in Fig. 32. The figure reveals that a mirror reflection may increase the vocal and investigative behavior of Zalophus. Each of the animals received two sessions with the mirror. However, Bibi demonstrated little reaction during the second session and the data from that session are not shown in the figure.



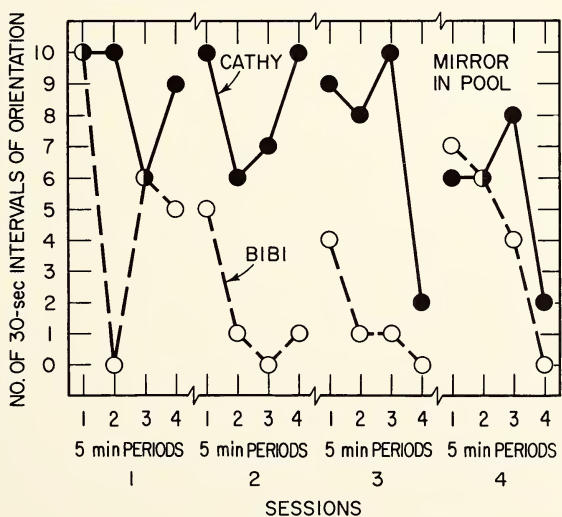
33. (a) (b) Orientation of a sea lion to back-to-back mirrors in the testing tank. (c) A sea lion about to bite the mirrors. (d) A sea lion in the act of turning sharply away from the mirror after making a "threatening run" at it.

The initial reaction from both animals was to orient to the mirror or test window for 10 or 15 sec., repeatedly leap out of the water and peer over the edge of the tank and then return to look at the mirror again. This sequence occurred three or four times and gave one the distinct impression that the animals were attempting to verify or locate the substance of the reflected "sea lion" image. This activity soon yielded to rapid swimming and porpoising accompanied by click vocalizations. Both animals would frequently swim approximately 5 to 6 m away from the test window, swing around and make a rapid "run" at the mirror, either pausing a few cm in front of it or making a sharp turn away. In many of these excursions, the animal was seen to move its head back and forth spasmodically in front of the test window as in a threat pattern. During these behavior patterns, clicks were often produced (sometimes accompanied by a stream of bubbles issuing from the mouth) when an animal was oriented either toward or away from the test window. The animals, particularly Cathy, then began to orient to the other windows. Only Cathy was observed to click during such orientations.

Many of the observations just described are, to a certain extent, reflected in the curves of Fig. 32. Bibi's clicking and orienting responses dropped sharply after the first 5-min-period without any recovery. On the other hand, even though orientation to the test window was maximal during the initial 5-min-period and declined thereafter, click production by Cathy did not reach a peak until the third 5-min-period, dropping sharply during the last test period. In contrast to Bibi, a second session with Cathy revealed considerable recovery of both clicking and mirror-orientation. Both behaviors decreased to what presumably was an asymptotic value. Interestingly, withdrawal of the mirror (post-test) during the first session resulted in an increased production of clicks and orientation



34. The course of intra- and intersession clicking vocalizations in the presence of back-to-back mirrors.



35. The course of intra- and intersession visual orientation toward back-to-back mirrors.

directed toward the test window. Subsequent recovery of these behaviors occurred on the following day during the first few minutes of the pretest. The foregoing effect may be viewed as a frustration reaction occurring when a significant "social" stimulus (mirror-image) was removed (1).

These interesting results with a mirror image led to a second "mirror" experiment in which two back-to-back mirrors were hung vertically over the center of the tank and submerged 71 cm below the water surface. The general procedure was nearly identical to the previous experiment except that it was unnecessary for E to get the animal to orient to the mirror.

Whereas none of the animals emitted underwater vocalizations during the pre- and post-test periods, all three immediately oriented and produced underwater click vocalizations upon initial exposure to the suspended mirror (see Fig. 33). Following an initial burst of clicks while approaching the mirror, Sam remained silent and showed no further interest in the mirror. The results from the other two sea lions are shown in Figs. 34 and 35. Again it is clear that there is a considerable degree of association between orientation to the mirror and production of click trains. The most salient features of these curves indicate that both orientation and clicking: a) decrease within each test session; b) recover between sessions; and c) generally decline over sessions. Note that all animals were generally more responsive when the mirror was in the tank than when it was covering a window outside the tank. In addition to clicking vocalizations, sharp cracks and whinny sounds were produced by Bibi.

All behavioral patterns occurring when the mirror was presented at the window were repeated with the mirror in the tank. In addition, the animals contacted and manipulated the mirror by pushing it with their noses, biting, and occasionally slapping and clasping it with the front flippers.

Summary and discussion. In these studies social and novel stimuli were found to elicit underwater click vocalizations from the California sea lion. In general, these experiments have confirmed the notion that clicking and other types of underwater vocalizations by Zalophus are associated with this animal's social and investigative responsiveness and are, therefore, related to a high level of behavioral and presumably physiological arousal. Although the vocal behavior of all animals tested was considerably increased above a base-line level under conditions of social interaction, only two of the animals showed an increased vocal responsiveness in the presence of a "mirror" stimulus, and only one animal's vocal responses appeared to be substantially affected by a large, "strange" object. This type of inter-animal variability in connection with Zalophus' clicking vocalizations has also been found in signal detection and discrimination tasks. Since the most vocal animal in the experiments (Cathy) had previously been the least vocal animal of the trio until it had been conditioned to vocalize, it may well be that the threshold for eliciting underwater vocalizations is decreased as a function of previous learning.

Welker (72) lists a few prominent features which tend to characterize play and investigative behavior: a) response to novelty; b) habituation; c) recovery. All these principles have been amply demonstrated in connection with Zalophus' investigative behavior as reflected by measures of visual orientation and specific object contact. In addition, these studies showed that the underwater click vocalizations of Zalophus also conform to these principles. Thus, clicking has been shown to occur in a "novel" situation, to habituate, and to recover from habituation. In fact, the curves for Zalophus' underwater clicks shown in Fig. 31 bear a resemblance to the chimpanzee object-contact curves obtained by Welker (71). Moreover,

the frequency of occurrence and the type of investigative behavior displayed by Zalophus appear to be similar to those shown by other modern Carnivora (24).

VII. Does Zalophus Rely on an Active Sonar System
for Purposes of Object Detection and Discrimination?

A. Discrimination Tests

Previous underwater discrimination tests designed to demonstrate Zalophus' ability to discriminate between circular steel discs of different sizes or objects of different sound-reflecting characteristics by means of active sonar alone have all proved negative (59). During these tests, in order to permit the E to make detailed observations of the animal as it swam toward the target area and at the same time to eliminate visual cues, sea lions were forced to make their discriminations 1.2 to 1.5 m from the targets. This testing procedure may not have been adequate for meeting the needs of Zalophus' active sonar system especially if this system, assuming it is operational, is used primarily at short ranges as indicated by Schevill, et.al., (57). However, a new technique was developed which eliminated visual cues, allowed detailed observation of the animal in the act of making a discrimination, and still permitted the animal to approach as close to the targets as was necessary prior to making the indicator response (striking the target). This technique allowed Zalophus to sample the echo characteristics of each of the targets for as long as it wanted and from any position in the test tank.

The technique is based on the assumption that an air-plexiglass target, consisting of two circular discs of 0.32-cm-thick plexiglass laminated in such a manner as to leave a 0.32 cm air space, forms an excellent impedance mismatch under water and offers a far stronger echo

than a 0.96-cm-thick plain plexiglass disc (22) of equal size and shape. Since the two targets were painted black, they appeared (visually) identical and testing of the California sea lion's ability to discriminate between inanimate targets by means of sonar alone could therefore be conducted in relatively clear water.

The animal used in the study was Bibi. Prior to the experiment proper, the animal was pretrained to emit a series of clicks which terminated only when it pressed against the target. During pretraining a single air-plexiglass target was presented and Bibi was reinforced after each "clicking" trial. Following pretraining, the animal was presented with 50 test trials per day for 21 days intermixed with 25 "sample" trials. The sample trials were simply presentations of the single air-plexiglass target in a center position. The test trials consisted of simultaneous presentation of the air-plexiglass target and the plain plexiglass target, randomly positioned to the right or left. During this test there was no barrier or stimulus divider. Therefore, the sea lion could and did move back and forth between the two visually identical targets, in order to examine each prior to indicating its choice. Although both circular targets were 33 cm in diameter, the air-space surface area of the laminated target was 736.1 cm^2 . Only choices of the air-plexiglass disc were reinforced with fish.

The animal's performance remained at a chance level (51% correct responses) throughout the course of 2050 test trials. This occurred despite the fact that the animal emitted click trains on virtually every trial. During a typical test trial, the animal would begin clicking as soon as the two targets were presented. Clicking would continue as the animal approached to within 15 to 61 cm of a target. Frequently

moving back and forth between targets while producing a continuous train of clicks until a final choice was made, the animal often appeared to be sampling or perusing the targets. However, on the basis of the results, it would appear that this behavior was a method of "visual sampling" and not "auditory" or "echo sampling." In other words, the sea lion apparently persisted in a futile attempt to detect some visual difference between the two targets.

One of the significant sonar responses of the bottlenose dolphin is that of "auditory scanning" (31), i.e., the continuous oscillation of the head at about 5° on either side of the median plane. Although this scanning movement occurs repeatedly while the dolphin emits a train of clicks and is swimming toward a target in turbid water, such behavior was rarely displayed by the sea lion.

The position of the sea lion, while it was still emitting clicks and just prior to indicating its target choice, was such that the signal (echo from the target) to noise (tank reverberation) ratio should presumably have been favorable for accurate detection and discrimination. Since the crucial aspect of any active biological sonar system is the degree of attention paid to the echo information, these results suggest that Zalophus does not habitually or innately "pay attention" to such available echo-information. On the other hand, it may be argued that since these tests permitted the animal its full visual capabilities, reliance on or the seeking of visual cues interfered with the animal's auditory attention processes. For this reason 500 additional test trials were given with underwater visibility reduced to a distance of approximately 1.8 m. Again the animal's performance remained at a chance level with 47% correct responses.

B. Feeding Tests

On several grounds it may be argued that although Zalophus did not

on the basis of active sonar, discriminate between the sound-reflection characteristics of different inanimate objects, it can detect and quickly find food fish by such means (50,51). Several tests of this hypothesis were conducted. In one such test, each of three California sea lions was separately allowed to view a single whole dead herring (about 25 cm in length) being thrown into the testing tank filled with clear water, and then was immediately permitted to enter the pool. This procedure was replicated ten times for each animal with the same result, that as soon as an animal entered the pool it caught and ate the herring. Following these clear-water tests, visibility in the water was reduced to a distance of approximately 10 to 20 cm, and each animal received 10 additional trials in turbid water. After draining the pool, from 6 to 9 untouched fish were recovered. Underwater sound monitoring during both clear and turbid water testing revealed the complete absence of clicking sounds.

Further tests with live fish yielded similar results. Thirty live mudsuckers (Gillicthys mirabilis), about 13 to 15 cm in length, were thrown into a tank of perfectly clear water. After watching the fish being thrown in, sea lion Sam immediately entered the tank and caught and ate 18 fish during the first 15 sec., 9 during the next 15 sec., and 3 during the last 6 sec. Thus, Sam ate 30 mudsuckers within 36 sec. Following this the animal was taken out of the tank and the underwater visibility was reduced to a maximum distance of approximately 20 cm. After being shown 30 additional fish scattered around the tank, Sam was reintroduced and remained in the pool for a period of 135 sec. The animal was, therefore, in the tank during the turbid-water condition more than three times as long as during the clear-water condition. After draining the pool, 17 untouched mudsuckers were found; indicating that Sam had caught and eaten only 13 of the 30 live fish during a period of 135 sec. In order to be

sure that Sam was not food satiated during the turbid-water test, the tank was refilled and the clear-water condition was repeated with 9 mudsuckers being thrown in. Sam caught and ate all 9 within 10 sec. of reentering the tank.

This same experimental procedure was repeated with sea lions Bibi and Growler with virtually the same results. Neither Sam nor Growler produced any clicking sounds in either clear or turbid water. Bibi, however, did produce rather long trains of clicks in turbid water, but performed no better than the "nonclickers." In summary, then, three California sea lions were considerably more efficient in their catching and eating of live mudsuckers in clear water than in extremely turbid water. Furthermore, two of the three animals were still capable of finding almost 50% of the available fish without emitting a single pulsed sound.

In order to determine whether the sea lions were capable of finding "all" the mudsuckers in turbid water, permitting a maximum visibility of 20 cm, Bibi and Growler were separately placed in the tank under such conditions with a total of 40 mudsuckers for a period of 50 min. Again, underwater monitoring revealed click emission by Bibi but not by Growler. Draining of the tank indicated that each sea lion had caught and eaten every fish that had originally been placed in the tank with it. Thus, given long enough time, Zalophus was capable of detecting and catching live mudsuckers even when the visibility was extremely limited. Since the mudsucker is primarily a bottom-dweller, it may be presumed that each of the sea lions made an exhaustive visual, tactile, or olfactory search of the bottom of the pool. The mudsucker is not known to produce loud sounds (Marine Poland Fish, personal communication) and it is therefore unlikely that their detection by Zalophus occurred on the basis of passive

sonar--although this remains a possibility. At any rate, these experiments do suggest that Zalophus is much more efficient in finding food by visual means than by active sonar, and that it can find live fish under extremely poor visibility conditions regardless of whether it produces sound pulses.

In summary, Zalophus has failed to demonstrate active sonar under conditions which would logically motivate its use. It has failed to use sonar to discriminate between inanimate objects or when seeking live or dead food fish. Although these findings cannot be interpreted as a proof that this sea lion has no sonar system, they raise a question as to the degree to which these animals rely on such a perceptual tool and the conditions which must prevail before it is brought into operation.

VIII. Concluding Remarks

A program of laboratory research has been conducted to shed light on the sensory and perceptual avenues used by the California sea lion (Zalophus californianus) for purposes of gaining information about its underwater environment. Demonstrations establishing the use of active sonar by the porpoise (Tursiops truncatus) and other cetaceans as a dominant perceptual instrument have led students of marine mammal behavior to suspect that Zalophus, as well as other pinniped forms, is also endowed with the ability to generate a sound signal, listen to the resulting echoes, and thereby detect and discriminate between different underwater objects. This was especially true once it was demonstrated that Zalophus was capable of producing sounds under water which had certain characteristics in common with the sonar clicks of the porpoise.

Results of laboratory studies described in this paper indicate that the California sea lion has rather good underwater visual acuity and is proficient in tasks involving visual form perception. Further data and

observations on their system of visual orientation suggest that Zalophus relies heavily on visual cues for the purpose of making underwater detections and discriminations. Although tests of underwater hearing are still at a preliminary stage, results so far indicate that Zalophus' perception of audio-direction is nearly as acute as that of the porpoise, Phocaena. On the other hand, controlled tests designed to demonstrate the use of an active sonar system by Zalophus have provided only negative results thus far, suggesting that its active sonar system, if it is operational, is rather primitive compared to that of the porpoise.

The question then arises as to the biological significance of the sea lion's clicks and other underwater vocalizations. The view I have taken is that clicking is part of a single system of calling which is elicited by stimulus conditions arousing intense or prolonged attention. This approach has been modeled after that of Andrew (3,4,5). Thus, it was suggested that underwater click production is related to a general arousal or activation of Zalophus as well as being one aspect of the orientation reflex (49,66). Studies showing that clicks occur under experimental conditions designed to produce intense alerting responses and organismic states associated with conflict and frustration tend to support this argument. Moreover, the finding that clicks and other apparently more intense vocalizations are associated with social interactions and investigative behavior gives further confirmation to this hypothesis. These results combined with the findings that click vocalizations are individually distinctive and readily subject to modification suggest that the vocalizations play a role in the underwater communication system of Zalophus.

Although clicking and other underwater vocalizations may be elicited by numerous unconditioned stimuli, experimentation has shown that clicking in Zalophus can be conditioned and that such conditioning appears to lower the threshold for the future evocation of such vocalizations. Since relatively little is known about the causation and development of sound production in those mammals that demonstrate a prevalent use of an active biological sonar system, e.g., bats and porpoises, it would seem quite desirable to determine what part learning plays in this process. I believe that studying the development and causation of click emission in pinniped forms may possibly give us information relevant to the genesis of biological sonar not only in pinnipeds, but possibly in other mammalian forms as well, particularly the cetaceans. This would be especially true if selective pressure were such that certain pinniped forms were currently in the process of evolving a biological sonar system. That learning may play a role in the ontogenesis of the bat's sonar system (Myotis lucifugus) is suggested by Vincent, who states that "...the greater the skill of a bat at avoiding obstacles, the fainter is the audible component of the sound it emits. In the same way, this low-frequency part of the pulse is more important in young bats than in adults (learning perhaps)." (69, p.188). These speculations make us increasingly aware of the need to conduct developmental as well as comparative studies of the animal sonar system.

Finally, since it is widely recognized that various species within a taxonomic order or family develop diverse adaptations according to their particular ecological niche, it would not be surprising to find that certain pinniped forms may rely on an active sonar system to a much greater extent than does the California sea lion. A likely candidate is the Weddell seal (Leptonychates weddelli), which produces a great variety of underwater

sounds (52) and is capable of diving to depths as great as 600 m under the ice (37) where no light can penetrate.

IX. Summary

Reports suggesting the efficient use of active sonar by the sea lion, Zalophus californianus, have led to research aimed at determining their underwater perceptual capabilities and the factors influencing their emission of "sonar" clicks. Zalophus has relatively good visual acuity and is capable of discriminating and classifying a variety of stimulus shapes. Perception of audio-direction by Zalophus is nearly as acute as that of the porpoise, Phocaena. However, tests of the use of active sonar by Zalophus have yielded negative results suggesting unfavorable comparison to the sonar of the porpoise.

In addition to clicks Zalophus emits other underwater vocalizations including barks, "buzzes", "cracks", and a "whinny" sound. Clicks are likely to occur during difficult detection and discrimination tasks as well as during social encounters and encounters with "novel" stimuli, e.g., a mirror. All these stimulus situations appear to have the common characteristic of arousing intense or prolonged attention. Moreover, underwater click emission is subject to control by means of operant conditioning techniques. These studies point to the need of conducting developmental as well as comparative studies of the animal sonar system.

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Footnote

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DISCUSSION

by

D. KENSHALO

There are at least two different ways in which the subject matter of this session can be viewed. Dr. Neuweiler has implied both of them. The first point of view is that in which stimulation of other sensory systems may influence, either for better or for worse, the functioning of the auditory system. The second viewpoint is that of the extent to which the active process of echolocation adds to an organized knowledge, gained by the other senses, including audition, of the environment.

With respect to the first point of view, that of the interaction of sensory modalities, Dr. Neuweiler has pointed out the immense amount of interaction which must take place between the various sense modalities in the reticular formation of the midbrain, thalamic nuclei, motor and sensory cortex. Studies of the activity in single cells in all of these structures have shown that they respond to stimulation of several of the senses. As well as this convergence of several sense modulations on a single central nervous system cell, there is also a divergence. Stimulation of a single sense modality will produce activity in widely separated parts of the central nervous system (3). This suggests that one should expect

to find a considerable effect of the stimulation of one sense modality upon another when behavioral (psychophysical) measurements of the performance of one of them are made. However, when these measurements were made, the effects of stimulation of a different modality upon visual acuity, or absolute thresholds of several of the senses, showed a small facilitation, if any effect was produced at all (8). The effects have been found to be marginal, at best, and may simply have been the result of added concentration on the task due to the distraction of the additional sensory stimulation, rather than the result of a true interaction. There are some examples of interactions between several forms of stimulus energy, for example, the effect of temperature of the solution upon the gustatory threshold or the effect of skin temperature upon vibratory sensitivity. It is not likely, however, that these are due to interactions in the central nervous system between the neural messages but it probably takes place at the receptor level. So, in spite of the electrophysical evidence which suggests that activity in one sense modality should affect another, behavioral evidence shows that interaction is marginal, if it occurs at all, in such simple sensory functions as acuity and threshold (8).

The other view of sensory interaction is the extent to which active echolocation augments information about the environment received by the senses. Here, it seems

from Dr. Neuweiler's review, there is convincing experimental evidence that only the Microchiroptera depend heavily upon echolocation as a primary system for spatial orientation. Other mammals should be added to the list. Convincing experimental evidence has been presented (6) that the bottlenose dolphin, Tursiops truncatus, depend heavily upon echolocation for spatial orientation although evidence concerning the extent of their visual acuity is meager. Because of their vocalization, feeding, and escape habits (diving to depths where light is meager), it is tempting to include many other genera of Cetaceans in the group of mammals which rely heavily upon echolocation for spatial orientation. This field is literally unexplored, however.

There is little convincing evidence at the present time that other orders of aquatic mammals, e.g., pinnipeds, use echolocation for spatial orientation. Dr. Shusterman's excellent report (this symposium) of carefully controlled studies with California sea lions, Zalophus californianus, rules out any possibility that this species uses active echolocation for purposes of target location. They do appear to possess an auditory localization acuity (listening) at least as good as that of the dolphin. Insufficient evidence is presently available to warrant a general statement concerning the use of echolocation by other pinnipeds. Based only on reports of the feeding habits of the Waddell seal, it appears possible that they use some sort of active acoustic search mechanism, but this remains conjecture.

Several species of birds, e.g., some species of cave swiftlet and the South American oilbird, and one species of mammal, the Flying Fox Rousettus, rely on echolocation only when the other senses, primarily vision, are inadequate. With respect to the South American oilbird, which is a fruit eater, while vision may be of importance in its navigation, it seems reasonable that olfaction orients it to its food source. It is an untrue belief that olfaction in birds is poor. As far as I have been able to trace it, this erroneous belief arose from some observations by Audubon that turkey vultures were unable to locate carrion when hidden from their view and, further, picked at stuffed skins or outline drawings of animals. We now know, from electrophysiological measurements carried out largely by Dr. Tucker (9) at the Florida State University biophysics laboratories, that a wide range of species of birds, including blue jays, night hawks, warblers, sparrows, gulls, chickens, sparrow hawks, pigeons, quail, geese, turkey vultures, black vultures, ducks and crows, all show neural activity in the primary olfactory neurons to concentrations of amyl acetate as low as or less than those which will produce a response in the rat primary olfactory neurons. (Concentrations of 10^{-3} fractions of vapor saturation at 20° C). The olfactory neural information is available. The next question is whether the bird uses or is able to use it. Only behavioral studies can give that answer. Dr. James

Smith, of the Florida State University psychology laboratories, together with Dr. Tucker (5), have succeeded in producing reliable changes in the pecking behavior of pigeons when concentrations of amyl acetate, comparable to those necessary to evoke an electrophysiological response, were introduced. This is of particular interest because previous attempts to condition a response to olfactory stimuli in the pigeon have generally failed. It suggests that until now we have not known how to ask the question in behavioral experiments. This and other evidence strongly suggest that birds can obtain information via the olfactory sense but their generally excellent vision makes this sense the primary information avenue.

As Dr. Neuweiler has pointed out, the structure of the eye is obviously well suited for portraying the spatial dimensions of the environment and from our own experiences we know how heavily we depend upon vision for effective operation in this space. Yet we have positive evidence that at least two species of mammals are able to operate very effectively in this space without the use of vision. Their effectiveness in the food search or in avoiding obstacles is not appreciably impaired when vision is denied (4, 6). Both porpoises and insectivorous bats have central auditory pathways and brain centers which have developed to a much greater extent than other portions of the brain (4, 6, and 7). This suggests the development

of acoustic facilities, even beyond those of man. On the basis of the currently available information, one can only speculate on the direction which this development has taken. Bilateral neural damage of the human auditory cortex is known to produce profound deafness. Lower mammals, e.g., dogs, cats, and rats, can be made to respond to even faint sounds after bilateral temporal ablation suggesting that in animals below man, simple reflexes and conditioned responses can be handled by subcortical centers. Results of cortical extirpation on frequency discrimination of cats are less clear cut, although Butler, Diamond, and Neff (1) present evidence that even massive lesions in the cortical auditory areas did not impair frequency discrimination. Bilateral lesions placed in the cats' auditory association areas, however, produce some striking debilitations in auditory localization and tonal pattern discriminations, e.g., high, low, high, compared to low, high, low. These are the types of discriminations upon which bats and porpoises would depend in moving about in their environment and catching prey. As well as functioning in this capacity, the well developed cortex of these animals may provide a type of auditory spatial memory, as described by Dr. Neuweiler for bats, much as a visual spatial memory in man is experienced. In this connection, the rather poor auditory localization acuity of the dolphin, Phocaena phocaena, reported by Dudok van Heel (2), of $8 - 10^\circ$ is

surprising when compared to the 3° found in man (10). This may have been a function of the frequencies which he employed, 3500 and 6000 Hz, as well as the conditions of measurement which may not have allowed the animal to use its full capabilities.

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DISCUSSION

by
F. WEBSTERINTRODUCTION

The means by which animals use self-generated vibrational signals to evaluate their environment constitutes a large and expanding area of investigation. The portion of this area which deals with signals in the sonic or ultrasonic range is often called "sonar"--though the definitions of sonar are often extended to include passive listening and are sometimes limited to the use of water-borne signals. For example, according to Horton (23):

Systems whereby underwater acoustic energy is used for observation or communication are known as sonar systems. The word "sonar" has also come to be used to designate the principles and practices employed in the design and operation of these systems...

The term "echolocation" (15,55) refers to spatially oriented responses guided by echoes resulting from vibrational disturbances of a mechanical nature generated by the animal, regardless of their frequency. But animal echolocation or sonar involves many sensory and analytical interactions. The common view that the sonar system is concerned only with simple temporal or spectral analyses of direct echoes, with respect to some standard emitted signal, disregards many essential aspects of most functioning systems in animals. The present discussion makes no attempt to deal with complex signal-echo relations or with the details of signal analysis. Neither does it try to resolve

technical differences between "sonar" and "echolocation." Rather, it reviews briefly some of the areas of the animal kingdom where echolocation or sonar may play a role in orientation, and considers some of the relations which may exist with other sensory modalities or with formative mechanisms. It deals explicitly with the papers on the general subject by G. W. Neuweiler (29) and R. J. Schusterman (48).

The two papers under discussion report selected aspects of animal sonar utilization in relation to other sensory mechanisms. These inter-sensory interactions may be of several types. In some instances, for example, data from one sense modality contribute information which makes the other modality more effective. In others, one sense modality substitutes, in function, for another. Thus, when light fails completely, echolocation may take over the orienting functions normally supplied by vision. In still others, one sense modality may serve an alerting or directing function for other sense modalities. For some animals, of course, echolocation is the principal orienting mechanism with respect to the immediate surroundings--with vision, olfaction, etc., playing only limited supplementary roles. The present papers deal with different aspects of such relations, each representing somewhat different concerns and emphases.

The paper by Dr. Neuweiler is, to a large extent, a review of visual-auditory interactions in certain mammals and birds. Of chief concern are the questions: To what extent are the sonar system adequate for the animals' mobility requirements? Under what conditions and to what extent do other senses (chiefly vision) supplement sonar methods, or substitute for them? The paper by Dr. Schusterman, by

contrast, deals chiefly with a single species, the California sea lion, Zalophus californianus. It is concerned with such questions as:

How adequate are the emitted signals for the detailed environmental probings which characterize some of the animal's activities? What are the directional and frequency sensitivities of the animal's auditory system? When presented with a precise quantitative task (for example, the discrimination of two similar-sized targets) does the animal depend on its sonar system to make the evaluation? What other functions may the sonar-like vocalizations serve?

The two papers will be reviewed from several broad frames of reference.

In order to systematize such a review, approaches by way of three general questions may prove useful. First--To what extent is the potential realm of animal sonar or echolocation sampled, in terms of the animal kingdom as a whole? Second--To what extent are the categories of function normally associated with an echolocation system covered? Third--To what extent do the reported investigations provide useful foundations for understanding the basic nature and mechanism of echolocation functions?

SONAR AND RELATED SENSORY MECHANISMS IN THE ANIMAL KINGDOM

Before reviewing the possible range of sonar use in the animal kingdom, we must state what kinds of orienting information are being considered. As already indicated, the use of passive listening in mobility guidance is sometimes included as part of the sonar system. Under this broad interpretation, much of the domain of audition in most

animals would fall within the field of discourse. In the present discussion active sonar, rather than mere passive listening, is assumed to be the chief realm of interest--along with infra-sonic echolocating mechanisms in animals particularly sensitive to such disturbances. The self-generated water undulations of the whirligig beetle Gyrinus (16) are thus included, even though the frequencies fall below the sonic range for man and their detection is by a non-acoustic organ (3). It must be borne in mind, also, that partial echolocation of various types may play some role in many of the oriented responses of higher animals. Inevitably, such responses are influenced by a wide variety of other sensory mechanisms often overlooked in studies of echolocation. Indeed, the field of animal echolocation or sonar in its entirety is so extensive, and yet so inadequately explored, that only a crude sampling is possible within any reasonable scope of discussion.

Fig. 1 is a survey of selected mammals and birds in which active sonar or echolocation has been suspected or demonstrated. The various animals are listed in part by systematic position (in terms of phylogenetic classification) and in part by representative habitat. In certain instances stress has been placed on animals which spend significant portions of their time in underwater search or travel, since underwater habitats both at night and by day often demand orienting responses under conditions where vision is greatly limited. At the top of Fig. 1 are listed topics or questions which pertain to the use of the echolocation system and the possible role of other sensory systems. The regions covered by the two papers under discussion are indicated, to a first approximation, by separate enclosing lines.

Fig. 1. SONAR AND SOME SENSORY RELATIONS IN MAMMALS AND BIRDS

Left-hand columns: Examples of certain animals in which sonar has been demonstrated or suspected, ordered partly by habitat and partly by phylogenetic position.

Top designations: Sonar usage and possible sensory relations:

Conditions: types of situations tending to elicit sonar-type signals (e.g., for most spatial orientations, during extreme darkness, in special situations, etc.)

Nature: functional emphasis of sonar usage (e.g., short-range navigation, configural evaluation, obstacle avoidance, object recognition, etc.)

Em. Signals: compatibility between observed signals and the animal's guidance or evaluation requirements (e.g., in terms of frequency or wavelength relative to objects evaluated, pattern variations with problem, etc.)

Audition: corresponding aspects of reception and analysis capabilities of the auditory system (e.g., frequency sensitivities, threshold (θ) and intensity sensitivities, etc.)

Vision: possible visual sensitivities and other adaptations which may permit adequate visual function under conditions sufficiently adverse to suggest the need for collateral or substitutive guidance by other senses.

Olf.: olfactory capabilities which may at times provide primary guidance, supplementary indications or alerting functions which activate other guidance mechanisms.

T.K.T.: tactile, kinaesthetic and thermal indications which may play a number of primary or collateral roles in oriented guidance of an animal--particularly with respect to the immediate environment or in mediating between distance guidance and direct close-range effects.

Vibr.: various vibration sensitivities not mediated by the auditory system per se. (although chiefly received by tactile-kinaesthetic mechanisms in higher animals, in certain fish the lateral line system may provide echolocation-like functions for object sensing in conjunction with self-generated water disturbances.)

Misc.: miscellaneous sensory contributions to oriented guidance, most notably the role of the vestibular functions in integrating the significance of many sensory indications with respect to motion by the animal.

Mem.: memory functions which form essential aspects of oriented guidance: either in maintaining an immediate frame of reference or in providing stored representations essential to meaningful sensory evaluations.

Enclosed regions: The area covered by the main portion of Dr.

Schusterman's discussion is enclosed by the upper solid black lines;

that dealt with in Dr. Neuweiler's discussion, by the broken lines

of the two larger areas below. The weighted box under Pteropus vision

indicates the special significance attached to the visual dark

CL.	HAB.	ORDER	Examples	CONDITIONS	NATURE	EM.SIGNALS	AUDITION	VISION	OLF.	T.K.T.	VIHR.	MISC.	MEM.
S L A M M A M S	ABOVEGAL & GROUND	PRIMATES	Man Apes & Monk Lemurs Tree Shrews										
		DEMOPTERA	Fl.Lemurs										
		SIRENIA	Manatees										
		PINNIPEDIA	Walruses										
		CETACEA	Seals & SL Porp. & Dolph Whales										
	AERIAL	MICROCHIR.	Myotis Pisonyx Rhinoloph. Rousettus Pteropus										
		MEGACHIROP.											
		INSECTIVOR.	Hedgehogs Tenrecs Moles Shrews Water Shrew										
		RODENTIA	Mice Doormice Hamsters Rats Beavers										
		CARNIVORA	Otters Mink Muskrats										
B I R D S	CAVE-NESTING	UNGUATES	Hippopot.										
		MONOTREM.	Sp. Ant Eaters										
		APODIFORMES	Swiftlet										
		CAPRIMULGIF.	Oilbird										
			(Nighthawks)										
	DIVING & NIGHT-FLYING	PROCELLARIID.	Petrels, etc										
		PELICANID.	Cormorant, etc										
		PASSERID.	Swallows, etc										
		STRIGIFORM.	Owls										
		GAVIIFORM.	Loon										
B I R D S	DIVING & NIGHT-FLYING	SPHENISCID.	Penguin										
		CHARADRIID.	Auk										
		ANSERIFORM.	Ducks										
	DIVING & NIGHT-FLYING												

adaptations of this bat by Dr. Neuweiler. (The lines for Dr. Neuweiler's area are very approximate and include, for example, the water shrews which were not explicitly discussed.) The hatched line for porpoises and dolphins indicates the partial reference made to these major sonar users. (For discussion of other animals listed, see text.)

In presenting this tabulation, no pretense is made at completeness; neither has any effort been made to fill in the spaces indicated. Likewise, in pointing to the regions left untouched by the two papers under discussion, no criticism is implied, since the authors obviously had to limit the scope of their material in order to make any detailed coverage possible. The tabulation represents merely a suggestive outline of possible echolocation and associated sensory inputs with reference to a sampling of mammals and birds.

Starting at the top we note, first, that among the primates, one known echolocator is a human being deprived of vision. In this connection, certain aspects of hearing have been studied extensively. Less recognized, however, is the concomitant or collateral use of tactile, kinaesthetic and vestibular senses. A man in darkness or a man who is blind maintains a running dead reckoning of velocity and directional shifts by use of integrations of muscular feedbacks and vestibular indications. Moreover, tactile and kinaesthetic clues received via the feet keep many an individual on the beaten path in total darkness--even without the use of hearing. Among arboreal primates and Demoptera, for example tree shrews and flying lemurs, little is known about the possible use of echolocation under conditions of extreme darkness. Though any complete system of echolocation seems unlikely in these creatures, some partial use remains a significant possibility.

Listed after the primates are some marine mammals, notably of the orders: Sirenia, Pinnipedia and Cetacea--some of which are actually fresh water inhabitants. The Sirenia (Manatees and Dugongs) seem to have

largely escaped studies of echolocating functions; while, at the other extreme, some of the Cetacea are among the best studied of all echolocators (30). Because of the extensive reports on echolocation in the Cetacea, the present investigators touch on such data only for rough comparative purposes. However, the need for comparative studies of echolocating functions in sea lions and porpoises was clearly a major stimulus for the work carried out by R. J. Schusterman.

Dr. Schusterman's initial step was to select types of target discrimination tasks known to be handled successfully by certain cetaceans (25, 30). When turbid water was used, with partitions which excluded effective vision, the experimental evidence indicated that the animal's sonar-like system could not provide the required discriminations (47). In this connection Dr. Schusterman noted that, although the animal's auditory system appeared to have capabilities not too different from the porpoises (except for an upper frequency limit at roughly 40 kc), the emitted signals tended to be of the order of 1/10th the frequency and to reach only about 1/10th the repetition rate. By contrast, the animal's visual discriminations were excellent (49, 50). Vocalizations which the sea lion emitted were clearly related to uncertainty, novelty, arousal-level, frustration and social factors. Moreover, they were readily conditionable. The fact that they were variable, that they were used for unexpected or novel conditions and that they were so readily conditionable led to the suspicion that--for this species at least--an echolocation system might be in the process of evolving, but that in the present state of its development any echolocation function must be relatively crude with respect to the discrimination function tested.

It is important to note that the experiments were chiefly restricted to one type of experimental task. Moreover, they were largely limited to one species of pinniped and involved--as do most such tests--a relatively artificial set of surrounding conditions. Schusterman points out that effective sonar systems may well be characteristic of other pinnipeds, most notably the Weddell seal (Leptonychates weddelli). The suggestion has been made that the Steller sea lion and the elephant seal may also regularly make use of sonar functions beyond the "orientation-reflex" category (usually involving alerting or information-seeking mechanisms) which seem to characterize many of the sea lion's vocalizations. Moreover, even in the California sea lion, Poulter cites a number of situations in which the echolocation function appears to be the main guidance procedure for target pursuit (37,38,39). Of great relevance, also, is the observation that blind sea lions appear to survive essentially as well as those with full vision (39). Possibly these are examples of echolocation functions extended by learning. In any event, we must conclude from these various findings that the full role of sonar among the pinnipeds is far from being adequately understood at the present time.

As far as cetaceans are concerned, a fairly extensive literature exists. However, most cetaceans are difficult to bring into the laboratory; even the larger porpoise tanks tend to constrain the activities of a 30 meter whale! Here it appears that a really adequate comprehension of cetacean sonar must await the time when miniaturized devices, carried by animals in the wild, can perform functions now undertaken only in laboratory situations.

Tabulated next in Fig. 1 is the order Chiroptera, the only true aerial mammals. Long separated in evolutionary trends, the orientation systems of the Microchiroptera and the Megachiroptera have evolved along separate lines. The Microchiroptera are echolocating bats, all members presumably being descended from insect-catchers, though some now live off fish, nectar, fruit or the blood of large animals. The Megachiroptera are visual bats, and the few (of the genus Rousettus) that use echolocation do so only when the surrounding illumination falls to very low levels. In Fig. 1, a weighted box is drawn under the vision of the flying fox Pteropus. Dr. Neuweiler has made careful studies of Pteropus vision and has concluded that it is exceptionally well adapted for useful perception at extremely low levels of illumination. Indeed, a human observer might be fooled into the erroneous impression that effective vision must be impossible under conditions where the bat could actually make good use of it. If the same holds for Megachiroptera in general, echolocation would not be required for survival by most members of this sub-order, which characteristically live on fruit. As already noted, in Rousettus echolocation is used chiefly at extremely low illumination levels--notably the darkness of caves--and is produced with the tongue. The mechanism is thus basically unrelated to that used by the Microchiroptera.

To Dr. Neuweiler's discussion of the Microchiroptera, one or two remarks should perhaps be appended. The first concerns the diversity of signals and their modes of utilization among the various members of this sub-order. It has been pointed out (58) that the significant features common to the signals of all insectivorous bats are chiefly:

pulsed form, basic tonal structure and a rapid variability which keeps pace with the nature or solution of an echolocating problem. Among different bats, however, great diversity exists with respect to: carrier frequency, band-width, range of pulse durations, duty cycle, amplitude pattern, intra-pulse transitions, and such like. However, since these considerations are well covered by Griffin (17) and in the current symposium papers by Moehres (27) and Pye (43), no more need be said here.

A second remark concerns the nature of the instant-to-instant signal variabilities mentioned above. The rapid adjustment of emitted signals constitutes a major point of difference between natural and man-made systems of echolocation. One view, of course, is that such "dimensions" of variability constitute a method of compensation for the reductions in dimensionality and channel capacity which characterize the auditory system, as against the visual system. Another way of putting this is to say that advance significance is assigned to the information received at the cochlea by mechanisms which pre-categorize the incoming acoustical information in terms of instantaneous signal features and related response requirements, thus reducing the decision field which designates appropriate action. It is as though a certain set of switchings were set up prior to echo reception, so that given stimulus configurations would automatically produce three-dimensional categories of response suitable to a given instantaneous situation. One aspect of this procedure might be conceived as a sort of automatically adjusting filter-focus mechanism. Among the features cited in this connection are: the timing and structure of the emitted pulses, the action of the external ears, the action of the middle-ear muscles and the

cochlear coding adjustments, presumably mediated by the olivo-cochlear bundle. Most such functions obviously involve interconnections with other sensory systems (tactile, kinaesthetic, etc.) either directly or by way of memory functions. There can certainly be no doubt that rapid adjustments of the outgoing signals, together with pre-selecting mechanisms of the auditory system, provide methods for speeding the match between instant-to-instant requirements of action and the sensory mechanisms which direct the action.

Tabulated next in Fig. 1 are some of the ground mammals which often make use of underground burrows or other darkened regions: members of the orders Insectivora and Rodentia. Dr. Neuweiler points out that one form or another of active echolocation appears to play some role in the orientation of many of these animals--at least under certain conditions. However, by comparison with primary echolocators (e.g., Microchiroptera), both the echolocating procedures and the scope of the derived information are greatly limited. Clearly, the capacity to determine required jumping distance or the existence of an open end of a burrow might often constitute essential survival requirements for such animals. Self-generated sounds, vocal or otherwise, might thus have been expected to form part of their orientation mechanisms. In some instances, interpretation of ground vibrations may also contribute to a knowledge of surrounding configurations. Although evidence exists that some of the animals emit ultrasound and that many may make use of composite sound patterns they detect, Dr. Neuweiler makes it clear that much further experimental work will be required before the range and nature of echolocation procedures among such animals can be fully elucidated.

The role of other sensory modalities in spatial orientation also remains uncertain. For example, great diversity seems to exist as to the use of olfaction for orientation purposes. Undoubtedly, tactile impressions--particularly those received by way of the vibrissae--are often of particular importance. Kinaesthetic and vestibular memories appear also to be particularly significant. Dr. Neuweiler notes that many of these animals restrict most of their activities to relatively small spatial regions. Here, the animal's memory of local configurations may permit the use of marginal clues with very limited information content. Undoubtedly, sensitivities to thermal gradients, heat radiation, temperature and air currents often provide different aspects of the needed clues. The orientation problems of such animals are thus assumed to be far less demanding than those commonly encountered by the widely ranging animals which depend on keen vision or highly developed systems of echolocation.

The next habitat category listed in Fig. 1 is that of the mammals adapted for fresh-water dwelling or under-water hunting. Among the least investigated of this category are the various water shrews. Some are known to pursue fish actively (56) and some hunt at night. The category is not mentioned by Dr. Neuweiler because the existence of echolocation has apparently not been explored. These animals are mentioned here only because they are likely candidates for an echolocation function in spite of the fact that their external ears tend to be greatly reduced and their ear canals presumably protected by closure while under water. Just as the water shrews are water-dwelling representatives of the mostly land-dwelling insectivores, so the beavers

are water-dwelling members of the mostly land-dwelling rodents. Beavers have long been suspected of some type of echolocation--possibly in part by use of sharp slaps made with the flat tail. Again, because of inadequate evidence, Dr. Neuweiler omits mention of this family. Besides the insectivores and rodents, a number of carnivores (e.g., otters, mink, muskrats) are at least partial water dwellers and hunters. However, once again, their orientation and pursuit mechanisms remain relatively little explored. Of the larger mammals, a good candidate for underwater echolocation is the hippopotamus; but, as with those animals just cited, adequate evidence is thus far lacking. From this hasty glance at some water-dwelling candidates for echolocation we can only conclude that the field is almost totally unexplored.

Listed next are the echolocating birds: Steatornis (the Oil Bird of Caripe) and Collocalia (Asian swiftlet). As noted by Dr. Neuweiler, these are the only known birds which use active echolocation in flight and--as might be expected--they are the only birds known to locate roosts in the total darkness of caves. Dr. Neuweiler points out that--as holds with the bat Rousettus--echolocation in these birds is initiated only at such low levels of illumination that their normally excellent vision becomes inadequate. Click production tends to be reversibly correlated with illumination at these low levels. In other words, echolocation is a substitutive function: it takes over essential visual functions only when vision cannot be used. It is important to note, however, that flight in dark, confined spaces may not be the sole situation where echolocation or sonar of one form or another plays a role in the orientation or hunting of birds.

If passive listening is included--possibly with some marginal echolocating indications--the following categories or situations might enter consideration:

<u>SITUATION</u>	<u>EXAMPLES OR CANDIDATES</u>	<u>CONDITION OR LOCATION</u>	<u>INVESTIGATORS</u>
1. Limited environmental orientation under conditions of flight where vision is unusuable	<u>Steatornis</u> <u>Collocalia</u>	Dark caves	Griffin Novick Medway
2. Supplementary guidance to vision during the pursuit of aerial prey at night.	Nighthawks Swallows	Late dusk or night hunting	
3. Underwater echolocation for detection and pursuit of prey, and perhaps for obstacle avoidance.	Diving petrels Cormorants Diving ducks Loons Auks Penguins	Underwater hunting " " " " " "	Poulter
4. Primary passive listening to action disturbances of prey, with the possible collateral use of intermittent active clues for spatial evaluation.	Owls	Pursuit of moving prey	Payne
5. Transponder-type triggering or communication (in which another member of the species--or possibly a different "symbiotic" animal--provides orienting information).	Least petrel (with petrels or <u>Pizonyx</u> responding)	Location of roosting crevices at night	
6. Passive listening to total configuration of sounds (both direct and echoing) made by other members of the species.	Many birds	General location of roosting areas	

Little direct evidence has been obtained regarding the possible use of echolocation either in the aerial night hunters (e.g., certain nighthawks) or in the underwater hunters (e.g., diving petrels). However, Poulter (personal communication) has noted that some penguins are capable of rapid location of underwater food in total darkness under conditions where other collateral clues appear to be absent. Our own efforts to detect ultrasonic clicks during apparent hunting by night-hawks under conditions of low illumination have thus far yielded negative results. Further studies of possible echolocation during the pursuit of prey in darkness are clearly needed.

The work of Payne (34) has shown that the barn owl (Tyto alba) is capable of highly accurate captures of moving objects in total darkness---provided that the requisite kinds of sound are produced by the motion of the objects. No usable sound is made by the birds during such pursuits; but some question remains as to how the general spatial configuration of the flight space is evaluated. Experiments by Curtis (10) indicate that echolocation is not used in flight and that obstacles are struck at chance level when the owls are flown in total darkness. Clearly the owl's primary orientation sense in total darkness is passive listening, and if some marginal form of echolocation from self-generated sounds is used, it must play a very limited role.

Question has long been raised as to how birds return to a specific nesting spot when the features which identify a precise location appear virtually undetectable to human perception. The problem seems even more acute when the nesting location must be identified in darkness too dim for human vision. One obvious example is found in the least petrel,

which often nests in large rock slides on islands in the Gulf of California. The assumption has been made that when one mate returned early at night from feeding on the waters of the Gulf, the other mate (which had remained at the nest) recognized an identifying call, as has been observed with other petrels, and answered back (1, 2). One difficulty is that, in this situation, the requisite calls are often not detectable by human listeners. It has been noted, however, that in certain locations, such as Partida Island, the roosts are shared jointly with Pizonyx vivesi--the Myotis-like fishing bat which inhabits the region. Starting immediately after dark, and continuing with some variability thereafter, is an almost continuous barrage of clicks which are emitted by the Pizonyx remaining in the roosts. Some relation appears to exist between the arrival of birds and the density of clicks--but the nature of the causality has not been established. One hypothesis is that the returning birds emit ultrasonic clicks which trigger off the cries of the bats, and that these, in turn, provide guidance for the birds. Though the birds are capable of emitting low-intensity ultrasonic clicks with their beaks, this kind of inter-animal symbiosis seems to represent an unlikely kind of relationship. For one thing, the sensitivity of the petrels' hearing to sounds of the order of 20 kHz has not been established. Most birds have been found insensitive to sounds of such frequencies (6, 41). The possibility is mentioned chiefly to indicate another potential kind of acoustical guidance which might be interpreted as an indirect sonar function.

Dr. Neuweiler makes no mention of creatures other than mammals and birds. Indeed, below the mammals and birds, there is little direct

evidence of well-developed active sonar in the animal kingdom. This seems somewhat surprising since many other animals, both vertebrate and invertebrate, live and hunt actively in regions where vision is unusable, or virtually so. Such is clearly the case with numerous water living creatures: notably, certain of the fish, Amphibia, and arthropods.

In 1955, Griffin reported paired sounds from a deep marine source (14). He tentatively designated the sound-emitting creature an "echo fish" and suggested that the signals might be used for deep water echo-ranging in the ocean. Though many sounds have been recorded from other fish and from Crustacea living in the sea (28), echolocating functions within the range of sonar frequencies have thus far not been definitively established. Considerable interest, however, has focused on the lateral line organs of fish. These organs are highly sensitive to vibrational disturbances and may sometimes respond to the reflected effects of self-induced motions. Many fish, of course, also derive important guidance from highly developed olfactory systems, and a number have developed forms of sensory mechanisms of radically different types; for example, the use of internally generated electrical fields. As yet, however, the possible use of sonar in the lower marine creatures remains largely unexplored.

There is one specialized habitat, often characterized by complete darkness, to which a limited number of animal species have made special adaptations. The animals under consideration are the true cave dwellers, or "trogllobites." Selecting two reasonably matched fish-- one a true cave dweller and the other partially adapted to cave life-- Poulson (26, 35, 36) attempted to define the neural and sensory

differences. Initial conclusions were that in the true cave dweller the following functions had tended to hypertrophy: olfaction (with olfactory brain center more complex), lateral line system (with external receptors, or neuromasts, greatly increased in number and sensitivity; "vibration center" characterized by larger nerve cells), vestibular system (with both the peripheral and central mechanisms markedly increased in size). The true cave dweller also appeared to have a significantly increased short-term memory system and the capacity to find its way amidst obstacles without collision. Such a skill may derive from a form of active echolocation based on interpretations of water disturbances produced by the fins. Although such a comparison represents but a single and inadequately explored example of integrated sensory adaptations to darkness, it is nevertheless of considerable interest in the present context; and may well provide clues to certain kinds of adaptations likely to be associated with evolutionary deprivation of visual functions.

Before closing this rough survey of possible echolocators in the animal kingdom, mention should be made of the most numerous and diverse class of arthropods: the insects. The insects have evolved a number of specialized sensory systems, and it seems quite possible that several forms of echolocation will eventually be discovered. Obstacle detection by actively induced undulations at the surface of the water by Gyrinus (16) has already been mentioned. Of potential interest also are some speculations as to the possible use of some form of ultrasonic echolocation by those moths which are sensitive to ultrasonic frequencies. Noctuids, geometrids, and arctiids typically fly at night

and possess sensitive tympanic organs. One of their major survival problems is the escape from insect-catching bats, and the moths often go through a diversity of gyrations upon hearing the emitted signals of an approaching bat (45, 57). Frequently these gyrations are carried out close to twigs, pine needles and such like--and question naturally arises as to whether the moths always fly indiscriminately into such obstacles, or whether they may sometimes detect them before contact. When light is present, they often seem to skirt such obstacles without collision; but such avoidance is presumably guided by vision. If avoidance is also achieved in darkness, some form of ultrasonic detection might logically be implicated. One suggestion is that such moths could use the interval pattern produced by the time differences between direct hearing of the bat's signals and indirect hearing of echoes from nearby objects. Again, however, any evidence for such detection is yet to be obtained.

To recapitulate briefly: acoustical or vibratory orientation by the use of self-generated disturbances of the surrounding medium appears to play some role in the mobility guidance of a great diversity of animals. The fact that relatively complete acoustical guidance is limited to a few sub-orders (certain Cetacea and the Microchiroptera) has tended to obscure the partial role of such mechanisms in the activities of many other animals. In addition, the common misconception that echolocation systems function in essential isolation from other sensory and central processing components tends to give a distorted view of their true role. Various kinds of interaction and exchange have been noted. In some instances vision, olfaction or tactile

mechanisms provide guidance clues which supplement or partially replace clues from active echolocation mechanisms. Undoubtedly, infra-sonic echolocation mechanisms often provide orienting information in conjunction with other orienting systems; and passive listening certainly plays a frequent and essential orientation role in most of the higher animals which use echolocation (60). It is important to remember, also, that learning and memory constitute essential ingredients without which much of an animal's echolocating indications would be quite useless. The two papers under discussion have provided examples of these considerations; but they have dealt with them chiefly at the gross behavioral level, and they have covered only portions of the animal kingdom. Perhaps we know as yet too little about the detailed mechanisms of inter-sensory interactions to say just how an echolocation system operates in relation to other sensory modalities. However, the comparative behavioral approach--taken together with neurophysiological findings--seems likely to give increasing comprehension of how echolocation systems arise and how they come to work in an integrated way in conjunction with other mechanisms.

REVIEW OF ECHOLOCATION OR SONAR FUNCTIONS

The second question raised at the outset concerned the categories of function normally associated with an echolocation system. Up to this point, only limited reference has been made to the kinds of function which might logically fall into the field of discourse. One thing, however, is clear: the histories, both of man-made echolocation systems and of natural echolocation studies, have been

characterized by a tendency toward progressive increase in the scope of the functions or features dealt with. For example, the early stages of radar development were concerned with the mere detection of an airborne object by use of a continuous wave (CW) system (51). The introduction of pulsed radar immediately resulted in a pulse-echo ranging function, and angle determination followed directly. However, angular accuracy was poor, and early fire-control radars were commonly used in conjunction with searchlights. Angular evaluations normally called for some kind of servo antenna control, with timing and directional indications suitably linked to display presentations or fire-control mechanisms.

To be effective, of course, not only the instantaneous detection accuracy, but also the speed of operation and the predictive capacities of the system had to keep pace with the kinds of dynamic problems presented. Moreover, the resolution of multiple targets, the rejection of clutter echoes and the suppression of jamming interference had to be handled. Rapid and versatile central processing methods thus came to form essential components. Identification and classification of detected objects called for the association of active radar-evaluation with passive reception and with assigned memory functions. The IFF identification system was a good example. With increasing automaticity, evaluations of multiple airborne objects were sorted into classes, under computer control, according to their paths and functional categories. Interception commands, and associated tracking, were also integrated into the total radar picture. As the domain of radar expanded, so did the opportunity for interaction with functions beyond the strict core of echolocation proper.

Bypassing the details of radar systems, we may next consider the more general categories of function with which modern treatments of radar typically deal (5, 40). The following is a representative list of functions or categories discussed.

1. Detection and localization of objects, masses and boundaries (as of rain fronts);
2. Identification of discrete objects directly from echo properties;
3. Mapping of broad configural relations;
4. Evaluation of navigational indications (combining #1, 2 and 3 above with other information as an aid to determining a suitable course of travel;
5. Communication: the use of coded indications in the transmitted signal;
6. Direct tracking of moving objects;
7. Indirect tracking and configural evaluation: the use of reflected energy that has been transmitted from a source other than the immediate system;
8. Passive detection of signals that may be associated with a particular set of echoes (as used, for example, in the IFF identification system);
9. Information relay: as, for example, in the transmission of partial indications to a more comprehensive or central processing system.

In addition, specific categorization is often made of important considerations, such as:

10. Clutter rejection: the separation of desired echoes from undesired competing echoes;
11. Resolution of multiple objects (including separations of the figure-ground type); and
12. Noise suppression: the isolation of desired signals from disturbances that are largely unrelated, in detailed structure, to these signals.

Though the specific contexts of radar functions are often different from those tabulated under animal sonar or echolocation, there is a general parallelism between the categories listed above and the kinds of things which form parts of our more general concepts of the echolocation functions of animals.

As viewed from a biological point of view, the echo-locating requirements of an animal, such as an insectivorous bat (58), usually fall into categories such as the following:

1. Detection and evaluation of specific objects (commonly potential prey)
 - a. Detection: awareness of objects within range;
 - b. Localization: placement in range, azimuth and elevation;
 - c. Identification: as, for example, in terms of size, shape, texture, action;
 - d. Resolution: separation from other nearby objects or from background;
 - e. Evaluation of relative paths (often the basis for predictive capture).
2. Avoidance of discrete obstacles: the detection, localization and sometimes recognition of objects to be avoided.
3. Evaluation of configurations: a 'wide-angle' view of general configurations ahead insofar as they dictate or limit the immediate path of travel.
4. Short-range navigation: orientation with respect to landmarks, as a guide to maintaining a course of travel. (Range limitations are set by: (i) dispersion and scattering, which often introduce third and fourth power losses as a function of distance, and (ii) attenuation by surrounding medium which reaches several decibels per meter in air, though only about 1/200 as much in water at the ultrasonic frequencies of chief concern).

As was true with the radar functions listed, several performance considerations enter the biological picture. For example:

5. Clutter rejection (as in the pursuit of prey close to a complex of obstacles);
6. Separation of desired signal from competing signals from other emitters (usually other nearby animals of the same species);

7. Noise suppression (though unstructured wideband noises are uncommon in nature);
8. Time constraints (the common need to perform evaluations and direct action within intervals that are short relative to the maximum possible processing speed);
9. Predictive evaluation of relative motion (for example, the capacity to evaluate acceptable paths of pursuit, where target speeds approach pursuit speeds while pursuit paths are constrained by surrounding configurations).

Regarding the selection of echolocation functions used in their discussions, Dr. Neuweiler and Dr. Schusterman make little explicit reference to just which aspects of the total domain of sonar or echolocation are under consideration. From the context of his discussion, it is clear that Dr. Neuweiler is chiefly concerned with what we might call local orientation: the capacity of an animal to find its way about its immediate environment and avoid collision with obstacles. Sensory interactions are considered in terms of when and how they might add to the orienting sonar information or substitute for it. Dr. Neuweiler also touches on the role of memory, but points out that stored representations of sensory or perceptual impressions belong in a different category from the direct orienting or mobility-guiding mechanisms which form the immediate basis of sensory guidance.

Dr. Schusterman focuses much of his attention on one functional category: the identification of discrete objects. Little reference is made to the other categories of function which are typically considered part of the job of an echolocating system. However, Dr. Schusterman goes on to deal with important additional features of natural echolocating systems which generally escape consideration: namely, the formative or shaping functions. Actually, he considers

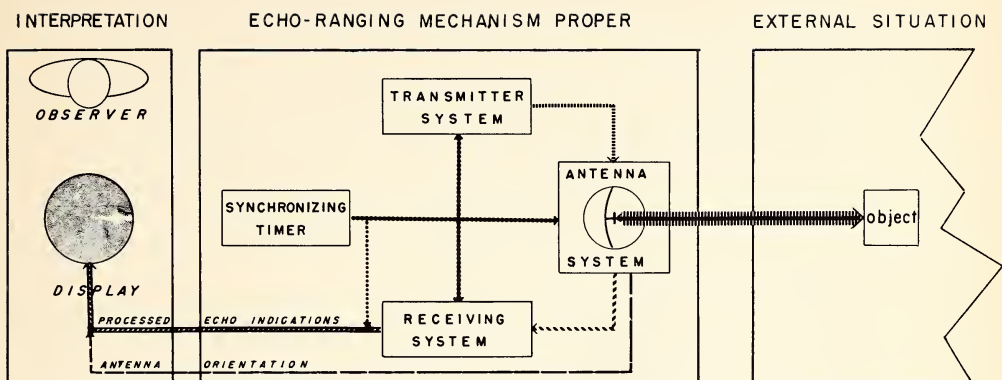


Fig. 2. SIMPLIFIED SCHEME OF PULSED RADAR AND ASSOCIATED CHANNELS

Central Echo-ranging Mechanism: Operation governed by four functional components:

- 1) Synchronizing timer, which sets up the pulse timing and synchronizes other system functions with respect to the transmitted pulses;
- 2) Transmitter system, which generates and shapes the pulses to be transmitted;
- 3) Antenna system, which (a) radiates electro-magnetic energy in a suitable beam, and (b) receives returning energy of prescribed categories from designated directions;
- 4) Receiving system, which amplifies returning indications and may carry out various processing functions.

External Situation: shown here as including only a single reflecting or scattering object, which returns a small portion of the transmitted energy.

Interpretation: here including only a PPI display which provides a rough two-dimensional "map" for human observer. (The line labelled "antenna orientation" indicates the linkage between antenna direction and display indications.)

two different aspects: 1) the role of conditioning and learning within the life of an individual, and 2) the possible role of certain individual variations in the evolution of echolocation in the species. These, however, are matters that more properly belong under the third question posed at the outset of the present discussion, and hence further mention of learning and evolutionary mechanisms will be postponed to the next section.

Before leaving the comparison of natural and man-made echolocation systems, brief reference should perhaps be made to the basic configuration of a representative man-made system. Since the papers under discussion are chiefly concerned with the first few radar functions listed (detection, localization, identification and, to some extent, mapping), a relatively simple representation provides an adequate description.

Fig. 2 shows a general plan of the ranging function of a pulsed radar system. Basic to the operation of such a system is an accurate synchronizing timer. In a pulsed system the timer normally does at least four things: it initiates the transmitted pulses; it simultaneously switches out the receiving channel (to prevent injury from the powerful outgoing pulse); it provides a time reference for the range-measuring function of the receiving mechanism, and it does likewise for the display devices. The transmitter system generates the carrier frequency, sets the pulse duration and the interpulse interval, and concentrates the output power into the moment of pulse transmission. The antenna system radiates the electromagnetic energy in a beam of appropriate form and width, and receives the returning echoes--sometimes

along with other indications, such as identification signals. In an angle-determining system, the antenna is positionable directionally and its mechanism gives an instantaneous indication of aim. Furthermore, if the antenna were of monopulse design (44), it might incorporate four slightly off-center receiving elements capable of providing immediate indications of the direction of an object with respect to the aim of the antenna. The receiving system amplifies the returning echoes, and it may perform a variety of selecting, filtering, correlating, motion-detecting and time-gating functions. It transmits appropriately selected and processed indications to the display system. If suitable angle-measuring and display functions are assumed, such a set of mechanisms thus generates a visual map--as represented, for example, on a PPI indicator. This display provides a basis for localization (at least in two dimensions), partial identification and configural mapping.

In the primitive scheme given, a human operator is assumed to make the pertinent observations of display indications, to integrate these with other data and to initiate suitable actions of command and control. However, when such functions are automated by the use of auxiliary devices and computer analysis, the scope of the total radar system becomes enormously extended. Prominent among such extensions are: the introduction of extensive memories, the use of sub-computing systems and the time-sharing of input channels. As indicated at the outset of this section, many comparisons of incoming data are made against stored reference data--some such data being previously placed there from external sources and some introduced and updated in conjunction with the

moment-to-moment progress of the current radar picture. By the use of time sharing, predictive evaluations, multiple storage categories, and association with collateral data, radar systems are able to resolve and keep track of many simultaneous targets and to carry out automatic control functions with respect to friendly targets to which control links are established.

In any comprehensive radar system, there thus exist many types of interaction beyond those involved in the simple measurement of distance and angle--which normally constitute only one peripheral phase of actual systems. In a number of instances, the various interactions have approximate analogies in the functioning of natural systems; and in some of these instances, the theory developed in conjunction with man-made systems has useful application to evaluations of corresponding aspects of natural systems (7, 8, 24). Some biologists, of course, are not fully acquainted with details by which advanced radar techniques can resolve complex environmental information; but, on their side, many engineers are not cognizant of the kinds of effective mechanisms biological systems may use in order to categorize complex perceptual data in meaningful ways--particularly with respect to the kinds of adaptive mechanisms which make possible the learning of complex patterns. One of the functions of the study of "bionic models" is to make useful bridges across such gaps.

FOUNDATIONS OF AN ECHOLOCATING FUNCTION

The third question raised at the outset, with respect to the papers under discussion, concerned possible contributions to our

understanding of the origin and nature of echolocation in animals.

The primary job of a sonar or echolocation system is to provide types of "mobility guidance" which enhance the animal's survival. Chiefly, in other words, such a system supplies indications which enable the animal to move about in meaningful and useful relation to its immediate environment. Like vision (and to some extent olfaction), hearing is a "distance sense." An active distance sense, such as echolocation, tells the animal about objects and configurations beyond the range of touch, thermal stimuli, etc., and can do so independently of energy radiation from the objects in question. Basically, any distance sense tells the animal something about what it may expect (in terms of close-range sensory shifts) if it carries out certain actions with respect to the indications received from a distance. The indications from such a sense might, for example, be interpreted in terms of how many steps or wingbeats lead to a detected surface, and they might even suggest how the surface should feel to the touch senses. Likewise, they might give indications of an opening which could be entered with a light brushing of external protuberances (such as vibrissae, wingtips, fur, or for man--clothing).

It is sometimes convenient, in experimental interpretations of oriented behavior, to define several broad categories of response. Among the more common are: (1) direct approach, (2) avoidance or retreat, (3) alerting or attention-focusing actions, (4) orientation with respect to some source, object or configuration, (5) initiation of exploratory behavior (or test actions designed to elicit further information), and (6) release of special categories of response (such as a catch maneuver). In echolocating animals, such categories tend to be

associated with somewhat different patterns of signal emission (9, 11, 15, 29, 30, 31-33, 39, 43, 55, 57, 59).

As already indicated, a distance sense arises out of the survival values gained by pushing the boundary of environmental information out from the animal; that is, away from the zone of direct contact and beyond the limitations imposed by simple tropistic indications. But the more direct meanings--and ultimately the survival importance--are inevitably in terms of close-range, or contact, senses, or events associated with them. Correlating bridges must always remain which connect the distance indications and the more direct sense impressions, on the one hand, and the actions which mediate between the two, on the other. The actions themselves, of course, also contribute sensory indications to the complex of relations. It is thus scarcely surprising that a diversity of correlating mechanisms should exist in the sensory integration systems of higher animals.

Dr. Neuweiler points to two types of neurophysiological findings which reflect such intersensory integrations. First, there are certain visual cells (as in the visual cortex of the cat) where non-visual sensory inputs (acoustic and somesthetic) converge; and second, there are, in the mammals at least, specific regions where indications from several sense modalities converge (e.g., midbrain reticular formation, thalamic nuclei and cortical association areas). With regard to the origin of cortical association areas, Geschwind (13) says:

"In the lower mammals connexions between regions of the cortex may arise directly from the primary receptive or motor areas. As one moves up the phylogenetic scale, these connexions come to be made between newly developed regions of cortex interspersed between the older zones." (p. 640)

Recent histological evidence (61), which relates to the control of visual aim from auditory indications, suggests that two ascending auditory systems may exist in the mammals. One system is basically an auditory-visual control or interaction system, primarily concerned with direction of the eyes with respect to received acoustical indications. This system includes the medial superior olive and is well developed in both diurnal and nocturnal animals which are primarily oriented by the use of excellent visual systems. Such animals include: the primates, and various large-eyed rodents and carnivores (e.g., chinchillas and cats). Cell counts in the medial superior olive are linearly related to cell counts in the N6 nucleus for eye-muscle control, for a variety of animals, both of the cone-retina (high cell count) and rod-retina (low cell count) categories. The medial superior olive is absent in the known echolocators analyzed: three kinds of echolocating bats and the dolphin Tursiops truncatus; also in the hedgehog Erinaceus europeus.

The other system appears to be a set of pathways and centers related to more diversified aspects of auditory information. This system includes the lateral superior olive, and at this level may be particularly concerned with various behavioral functions related to auditory localization. The lateral superior olive is strikingly developed in echolocating bats and in the dolphin; also in the hedgehog (an insectivore) and in some of the nocturnal rodents.

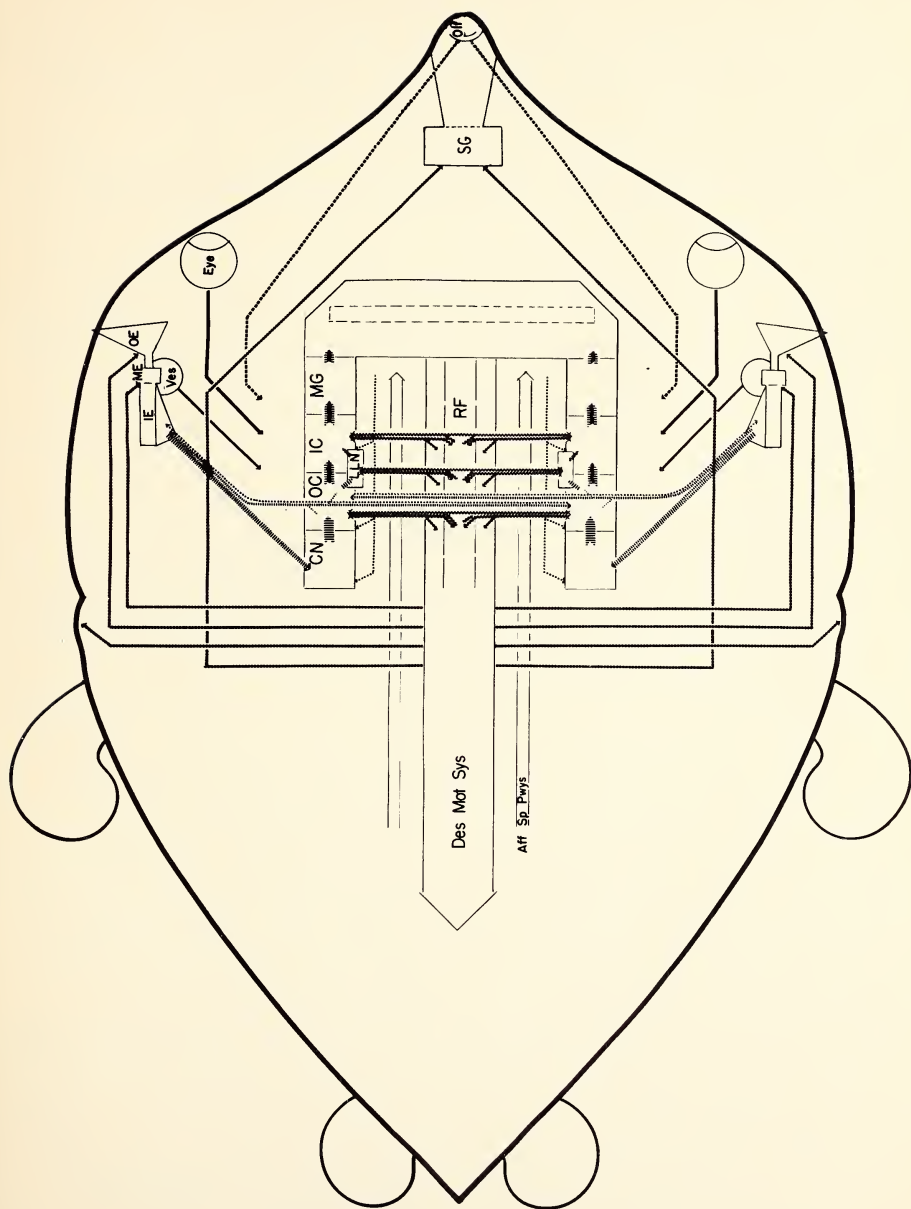
Fig. 3. SCHEME OF SELECTED MESSAGE CHANNELS IN HYPOTHETICAL ECHOLOCATOR
(Chirocetan microtornis)

Primary ascending auditory pathways and allied cortical functions are indicated by inverted "U" configuration at center. Box in light broken lines suggests coordinating memory functions. Successive ascending auditory centers are as follows: cochlear nuclei (CN), olivary complex (OC)--often considered, along with nucleus of lateral lemniscus (LLN) as a collateral rather than sequential set of centers, inferior colliculus (IC) and medial geniculate (MG). The development of higher centers (primary cortical reception area and association areas) vary greatly among different echolocators.

Other incoming and ascending pathways shown include: a) those from the other special senses (e.g., olfactory receptors, visual receptors and vestibular organs) and b) those of the numerous sense modalities carried by the afferent spinal pathways.

Four motor out-flows are indicated: 1) to the middle ear muscles, 2) to the muscles of the outer ear, 3) to the neck muscles which direct combined head-ear aim and 4) to the signal-generating mechanisms. An outflow via the olivo-cochlear bundle leads to the coding mechanisms of the inner ear and presumably governs features of peripheral reception. In addition, pathways of descending sensory control are indicated by dotted lines leading down to ascending auditory pathways.

Several main sets of cross-channels are indicated, which suggest left-right interactions at various levels. Numerous connections with the brain stem reticular formation (RF) are indicated, and outflows to the descending motor system from several levels are also shown. (For discussion, see text.)



It is inevitable that a higher animal should need to comprehend its world in terms of integrated sensory impressions related to the specific actions it makes, and that there should arise a variety of foci for such inter-sensory interactions. Moreover, in the higher animals, as the complexity of inter-sensory relations increases, stored "image patterns" come to play increasingly important roles in many types of oriented behavior.

To provide a very crude plan of selected organizational features in a generalized echolocating animal, the representation shown in Fig. 3 has been made. From even so rough a scheme certain features are immediately evident. For example, such a system is:

- (1) bilaterally arranged,
- (2) hierarchically organized,
- (3) characterized by multiple afferent channels, efferent channels, cross channels and message-combining regions,
- (4) functionally governed at several levels by intercommunications between immediate input messages, stored weighting functions, descending command and control indications, pre-set coordinating mechanisms, etc.

Furthermore, though not so evident in the scheme presented, much of the action of such an echolocation system takes the form of sensory-motor loops that are either fully or partially closed. In locating an insect, for example, a bat may turn its head and ears until its transmit-receive system is correctly aimed. The initial aiming deflection may, of course, be of the command or ballistic type in which a given binaural (or monopulse) input (4, 44) sets up a prescribed action pattern; this pattern, once initiated, being carried out without intervening control. There can be little doubt, however, that even such ballistic motions (and certainly the ensuing error-correcting actions) are monitored by proprioceptive indications.

Again, as with the antenna-directing control loops which

govern transmit-receive directionality, there are signal control loops which govern pulse structure and timing. Suppose, for example, a bat or cetacean possesses a ranging function which is most sensitive at a given pulse-echo separation or overlap (9, 20, 30, 31-33, 42, 43). Initial target detection may set off a pulse timing-shift designed to approximate the optimum pulse-echo relation. Though the pulse details and the pulse timing may be initially under control of a command function, it seems most likely that here, also, the desired relations are maintained with the use of proprioceptive feedbacks which successively modify certain assigned properties.

In Fig. 3, five such loops have been emphasized in terms of their efferent (outgoing) pathways: (1) the input coding control path (via the olivo-cochlear bundle), leading to the inner ear transduction-coding mechanisms, (2) the rapidly-acting path which governs contraction of the middle-ear muscles (21), (3) the paths which control the action and position of the outer ears at the two sides (46), (4) the paths (mentioned just above) which go to the neck muscles and control the general aim of the head and ears, and (5) the paths which go to the signal-generating mechanisms (also mentioned just above). Such loops are influenced, of course, not only by direct auditory inputs, but also by associated inputs deriving from many sources. Conspicuous among these are proprioceptive and tactile inputs from various regions--only crudely intimated in Fig. 3 by the arrows representing the afferent spinal pathways. Essential, also, are the vestibular inputs which govern much of the rapid control of motion, so important in most types of pursuit maneuvers.

Olfactory and visual inputs are also indicated, though such inputs may or may not enter the picture at any given time during the solution of an echolocating problem.

Highly important in many echolocating situations is the matter of response speed. Some insects, for example, are remarkably adept at making unpredictable and rapid shifts of flight path during the approach of a pursuing bat (45, 58). A flying moth can suddenly deflect its logically-expected course by as much as 15-20 cm in a tenth of a second. If a bat must have the moth correctly localized to within a volume 3 or 4 cm across, in order to seize it with a wingtip, then very little sequential neural processing can be carried out in the bat's nervous system between a given signal emission and a given set of motor actions that must be precisely guided by use of the returning echoes. In such a situation one must consider the essential times for echo-return, peripheral coding and conduction, organization of muscular control and the physical execution of resulting orders. With these times taken out, there remains time enough for only a few sequential synaptic transmissions in the central nervous system.

Such considerations immediately eliminate extensive filtering, correlating or iterative-type processes. Of the remaining kinds of processing methods that might lead to rapid, coordinated motor action, two might be mentioned. First, there are what we might call dispersive conditional probability methods. According to such methods, a given set of input patterns might be used to make a number of possible rough predictions. A suitable match with the next set of returns would immediately activate the best matching prediction, and the results

lead to assigned categories of motor action. Second, there are what might be termed multiple-input matrix methods, according to which a given response pattern (or pattern increment) would arise directly from a given input array over a prescribed interval. Such a procedure might be crudely analogous to the insertion of a given key into a number of possible locks. The box opened would contain the appropriate instructions for the action pattern which suited that key.

In terms of Fig. 3, terminal, reflex-type responses of the sort just mentioned would appear to be mediated by lower-level processes. It is clear from the figure that various kinds of interaction--including binaural interaction--might take place by the level of the olivary complex (OC). There appear to be outflows to the descending motor system, as well as various interconnecting functions by way of the brain stem reticular formation at this level and at the level of the nucleus of the lateral lemniscus (LLN)--which is well developed in the echolocating bats. If such animals as the bats possess disproportionate development of such centers, it may reflect the essential role of speed in various survival essentials.

In the bat, however, the most prominent auditory structure is the inferior (or posterior) colliculus. The studies of Grinnell (19, 20), Suga (52-54) and others (12) suggest remarkable sensitivities to time and frequency in this center. Undoubtedly, many of the complex evaluations made by bats are mediated, in considerable measure, at this level. Above this level the auditory receptive areas of bats are relatively undeveloped in comparison with higher mammals. At the same time, the capacities of bats to learn--even if slowly, and often crudely--

suggests that important functions related to memory and learning do occur at higher levels. Moreover, the bat--like other creatures--must function in terms of integrated sensory impressions involving all of the various sensory modalities. Presumably the vastly greater development of the higher centers in cetaceans reflects far more complex integrations--involving, perhaps, more extensive pattern analyses over time, greater interaction of stored inter-sensory representations and more versatile adaptive mechanisms. The scattered evidence we have suggests that interactions take place at many levels and in a variety of ways. But most details of such interaction mechanisms remain to be discovered.

What does this all-too-sketchy review tell us about the basic plan or nature of natural sonar functions? Obviously not much that is usefully concrete. Perhaps all we can say is that it has pointed to certain features which may be relevant to the effective operation of such sonar systems. Thus, it has stressed the organization into sensory-motor loops, in which multiple sensory inputs may be required to make the system effective. It has also pointed to the diversity of interaction categories which may be involved, and to the hierarchical design which facilitates speed of response where speed is crucial. Most of all, however, it leaves us with the realization that our knowledge is still in terms of incomplete fragments and that as yet we cannot formulate any adequately valid or integrated model of how such systems function (18). Dr. Neuweiler indicated certain areas where our fragmentary knowledge of sensory interactions was beginning to emerge; but until we know much more about specific mechanisms and system organization our views must

Dr. Schusterman's discussion deals with a very different aspect of sonar foundations. A major portion of his concern is with

the conditions which elicit, and perhaps extend, the sonar potential of pinnipeds--especially the California sea lion. Somewhat oversimplified, two of the main questions might be put as follows:

1) What role does conditioning and learning play in the production of underwater vocalization--and perhaps sonar utilization--in the life-span of an individual sea lion? 2) Do the individual variations in vocalization properties and propensities serve to further evolutionary increases in sonar usage within the species?

Evidence already cited suggests that the sea lion uses underwater echolocation for the guidance of certain tasks. However, neither the signal properties nor the frequency-range of the animal's hearing appear compatible with echolocating proficiencies of the levels reached by the advanced echolocating systems of certain cetaceans. At the same time, the sea lion's mode of life appears to be such that both individual and species survival might well be enhanced by increases in the effectiveness with which existing capabilities were utilized or selected.

Perhaps the most significant feature of the sea lion's sonar derives from the very fact that it is, in a sense, a skill on the evolutionary fringe, and one possessed by an animal with interesting versatilities and variabilities. Fundamentally, the sea lion is a visual animal, closely allied to the carnivores. Commonly it lives in clear water, where--as already noted--it is capable of excellent visual perception and discrimination (49). However, when frustrated by poor visibility, or when alerted or aroused in various ways, it tends to emit a variety of vocalizations. In Schusterman's experiments, the echoes from such vocalizations failed to provide the animals tested with any

capacity to distinguish between a variety of targets. However, as also noted above, Poulter's evidence indicates that the animal's sonar system can make certain kinds of discriminations, and is capable of effective guidance of target pursuit (39). Variabilities in such findings may come from many sources. Certainly, the degree of matching of experimental situations to natural conditions is often a significant and elusive one. In any event, the precise role of sonar functions in pinnipeds remains largely unsettled in the face of existing evidence.

One obvious focus of interest is on the methods by which the sea lion may push its limited sonar capabilities into the realm of survival importance. In this connection, the diversity of vocalizations produced under conditions of frustration, uncertainty, urgency, etc., have already been stressed. Perhaps the sea lion gains survival advantages by discovering how to put together certain subtle echo-patterns into perceptual entities. Perhaps, also, such psychophysiological advances lead the adaptive trends of the species--with compatible anatomical modifications following at a slower rate. And possibly, once again, it is the disconcerting variabilities, plaguing the consistency of experimental findings, which provide the most valuable clues to underlying mechanisms.

In concluding, we must point out that the papers under discussion were not basically directed toward an analysis of how echolocation systems arose or why they have taken the forms we now see. Such aspects have emerged chiefly as interesting sidelights to other issues under consideration. Perhaps, however, they have served to stress one thing: if we really want to discover the full details of animal sonar, we will sooner or later have to trace the evolutionary trends and developmental processes out of which the systems have come into being.

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ABSTRACT

Papers by G. W. Neuweiler and R. J. Schusterman discuss different aspects of sensory interactions related to animal sonar. Neuweiler reviews a variety of interactions in mammals and birds. Schusterman, focusing on a single species (the California sea lion), evaluates sonar capabilities relative to visual functions and investigates conditions eliciting sonar-like vocalizations.

The present discussion is a review in terms of: animal sampling, essential mechanisms covered and basic design functions clarified. Obviously our current knowledge of sonar contributions to animal orientation remains, in most respects, rudimentary. For example, many partial uses of sonar or echolocation are as yet scarcely recognized and the manner of interaction with related sensory systems very inadequately understood. In addition, the role of memory in sensory comparisons, and as a source of triggered intersensory images, tends to be overlooked. Of interest is Schusterman's suggestion that the sea lion may be on the evolutionary fringe of effective sonar development, with the animal's vocalization diversity and conditionability spear-heading the trend. Clearly, evolutionary models of sonar mechanisms are needed.

animal sonar
echolocation
sensory interactions

INTERCEPTION PERFORMANCE OF ECHOLOCATING BATS IN THE PRESENCE OF INTERFERENCE

by
F. A. WEBSTER

INTRODUCTION

The performance characteristics of animal systems are frequently compared with corresponding performance characteristics of man-made systems. Such comparisons, however, commonly lead to controversies between biologists and engineers. Thus, in comparisons of the object-detection capabilities of echolocating bats, two sources of controversy have been evident: 1) inappropriate comparison and 2) differences in the design methods and materials of natural systems as against those of man-made systems. Inappropriate comparisons have often characterized the analyses of a bat's range of detection and detection efficiency as against the detection performance of man-made counterparts (3, 4, 9). It is clear, for example, that the range of ultrasound in air is greatly limited by atmospheric attenuation; and hence comparisons of detection efficiency between the systems of bats and the man-made counterparts (water-borne sonar and air-borne radar), in terms of absolute distance, can be very misleading. Furthermore, comparisons that have been made of percentage capture scores for targets, under echolocation guidance, have sometimes failed to consider differences in basic parameters (1). For example, a bat's primary intent while hunting may not be to capture 100% of the targets detected,

but rather, to obtain a maximum amount of useful fuel (edible insects) with a minimum of risk and energy expenditure. Legitimate comparisons can be made only if corresponding requirements and related constraints are properly defined.

Comparative evaluations of the basic nature of biological designs, as against those of engineering systems, present more complex problems than do comparisons of the operation of defined mechanisms. However, before embarking upon a survey of interception performance under certain complex or difficult situations, some differences between biological and engineering design emphases should be made.

Biologists generally point out that living systems have features or capabilities which engineering systems cannot duplicate.. For example:

- a) Biological sensory and processing mechanisms are often micro-miniaturized by many orders of magnitude in comparison with corresponding engineering mechanisms and they may operate at less than a billionth of the power.
- b) Some sensory systems have extraordinary sensitivity to minute absolute stimulus magnitudes and to small shifts of magnitude.
- c) Auditory and visual systems of higher animals can deal with complexities and subtleties of pattern which engineering systems cannot approach.
- d) Living systems, in general, have highly effective couplings across the various boundaries related to their survival and thus achieve an autonomy of function not achieved by engineering systems.
- e) Animal processing systems can sometimes derive accurate outputs, with respect to complex stimulus configurations, even though the inputs may be approximate and diverse.
- f) The higher nervous systems of animals can deal effectively with types of unexpected situations which inevitably confuse mechanized systems.

Engineers typically counter such lines of argument with a number of contentions. For example:

- a) Most engineering components are so different from biological components that they dictate methods far removed from those of biological systems.
- b) Even if larger and vastly more power-consuming, electronic components generally surpass biological components enormously with respect to such features as: resistance to injury, unit accuracy and reliability, and speed of operation. (For example, items can be usefully retrieved from computer memory at rates approaching 10,000,000 items per second--many thousands of times faster than the sequential memory utilization speeds of animals.)
- c) Engineering methods are not frozen into limited categories of function by limitations of biochemical composition or evolutionary commitment.
- d) Even if biological systems can do things engineering methods cannot duplicate, engineering systems can do other things which biological systems cannot. (Examples are: high-speed and intricate logical reasoning, with associated decisions, and pattern recognitions involving large and accurate counts.)
- e) When they can be viewed in detail, the complex adaptive mechanisms in the nervous systems of higher animals will probably prove extremely inefficient in terms of the number of unit operations performed to gain a small increase in overall operating effectiveness.

This last contention incorporates an issue so central to biological design that brief additional comment is in order. If biological systems are conceived as arising out of simple governing principles, then these principles must act "in ignorance" of surrounding conditions and requirements. With respect to a given "goal direction" they may thus be construed as acting at random. Biological order arises out of the gradual and exceedingly "wasteful" consolidation of design patterns which prove meaningful in terms of stable modifications they introduce into the relations between a biological system and its environment. Granted that the design efficiency of natural systems may tend to increase as mechanisms that catalyze evolutionary acceleration appear, nevertheless systems with versatile design properties tend to be very inefficient at the outset. Since inefficiency of operation is

inherently abhorrent to engineers, the design methods of nature run contrary to their basic views.

If we look at the results of evolutionary operation on the guidance system of echolocating bats, we must conclude that the design methods--however inefficient in detail--must have proved effective in the end. Bats appear to have survived well over changing conditions for some 50,000,000 years or so (5). Moreover, as individuals they may survive, on the average, for 5 to 10 years, during which time they may fly many thousands of miles and capture, without errors of serious consequence, hundreds of thousands of insects which are often flying in the vicinity of potentially injurious objects.

When biologists point to the guidance methods of bats as effective systems, they are thus referring to their effectiveness in terms of the specific survival requirements of bats, not to their capacity to duplicate similar-appearing functions of man-made systems--though under certain conditions such comparisons may prove legitimate and significant (7). Biologists normally disregard the design considerations important to engineers and are little concerned with details of operating efficiency--as long as the overall accomplishments of the system in question are effective. Many engineers are also often willing to overlook sins of natural design and deficiencies of detailed methods--provided that the overall operation of the system achieves results difficult or impossible to duplicate in feasible engineering systems.

Of particular interest to communications engineers have been certain quantitative results on the capacity of bats to locate and avoid



FIG. 1. Capture and rejection of moth by Lasiurus borealis. The moth is about to be captured at the second flash, is in the tail pouch (formed by the bat's interfemoral membrane) at the third flash and is being rejected at the fourth flash. (Flash intervals here and in subsequent sequences are approximately 100 milliseconds, unless otherwise noted.) For discussion, see text.

obstacles in the presence of high levels of wideband, random noise (6, 7). Certain bats have been found capable of detecting faint echoes in noise when the signal-to-noise ratio appeared to be worse than the level required for an "ideal detector." Actually, such bats not only incorporate highly effective mechanisms for signal processing; they are also able to make use of a variety of auxiliary procedures and correlations which enhance their detection capabilities.

Efforts to make corresponding measures on pursuit performance in the presence of noise have encountered complications not met during obstacle avoidance experiments. The presence of wideband noise appears to inhibit the detection and pursuit efforts of most bats tested to such an extent that useful performance measures have been difficult to obtain. One interpretation is that intense wideband random noise is an unusual masking stimulus in nature and that the bat's system has to adapt its processing methods to deal with it. Experimental procedures used during pursuit tests have thus far not allowed for this. A second interpretation is that bats tend to treat such noise as an adverse signal. A number of insects, suspected of having (or mimicking) such obnoxious characteristics as clinging spurs or offensive taste, are capable of emitting noisy clicks. Tests have shown that such clicks--or approximations to them, even at very low sound levels--tend to produce relinquishment of target pursuit (2). Bats often reject captured insects for reasons that are not yet clear (Fig. 1). Further work is needed before any useful evaluation can be made of the true pursuit capabilities of bats in the presence of wideband noise.

Casual observations had suggested, however, that there were a number of situations in nature where bats executed effective pursuits

in the presence of a variety of interfering conditions. These included (14):

- a) the presence of multiple targets, sometimes requiring close resolution between adjacent objects--possibly sometimes involving discriminative evaluations between alternative selections.
- b) the existence of strong "clutter echoes" from large objects or surfaces close to a small target.
- c) the occurrence of complex clutter echoes which might approximate the echoes of the desired target and might at times come from objects that were closer to the bat.
- d) the presence of intense signals similar to the bat's own emitted signals--notably those emitted by nearby members of the same species.
- e) the presence of constraining configurations, such as leaves, twigs and branches, which might require comparative evaluations of:
1) target location and probable trajectory, 2) background configuration relative to the estimated trajectory and 3) own path with respect to both of the above.
- f) the possible existence of small, dangerous obstacles, such as sharp twigs or thorns.

In the next section a few selected samples of the response of bats to some of these situations will be given, and in the final section a few considerations which relate to such results will be considered.

SOME EXAMPLES OF INTERCEPTION PERFORMANCE IN THE PRESENCE OF INTERFERENCE

Multiple targets

The natural targets of bats often occur in fairly dense clusters. Certain insects, for example, travel in swarms; and it has been conjectured that bats obtained their food by passively listening for insect swarms and then flying through them--target captures being guided from tactile contact of insects with the flight membranes (15). Present evidence does not contradict the possibility that this method

may sometimes be used. However, it does demonstrate that bats are capable of isolating and capturing individual members of silent clusters of targets.

Figure 2 shows a red bat (Lasiurus borealis) seizing one out of a cluster of 32 mealworms, projected upward from below (by use of a solenoid-driven "gun"). Although the bat obviously did not have to deal with echoes from the lower targets of the cluster, roughly half were close enough to the chosen target to produce potentially confusing echoes.

Figure 3 shows the same bat in the process of capturing one out of five potential targets. The mealworm farthest to the left is just entering the tail pouch of the bat at the last image.

Figure 4 illustrates the separation of a mealworm from a 3 mm sphere, within roughly two centimeters. The catch here makes use of a backward somersault; and in the next-to-last image the end of the mealworm can be seen hanging out from the edge of the tail pouch as the somersault reaches completion.

Strong clutter echoes

Figure 5 shows a bat (Myotis lucifugus) correctly tracking a mealworm up to the surface of a smooth sphere (of about 1 M diameter). Obviously the approach angle is such that much of the sound reflects away from the bat. At the same time, the radiation pattern of the bat's signal, at terminal pursuit frequencies, is such that a very large clutter echo must occur in such situations. The bat's accuracy appears unimpaired, the mealworm being between the bat and the sphere as the bat puts out its wings, presumably to slow its speed, in preparation for contact with the surface.



FIG. 2. Capture of one out of 32 mealworms by Lasiurus borealis.

Capture is being made at flash #3; the target is then retained momentarily in the tail pouch (flash #4) before being seized with the mouth (flash #5). (This sequence is Fig. 10 of ref. #13).



FIG. 3. Capture of one out of 5 mealworms by Lasiurus borealis.

The upper image shows the selected mealworm just entering the tail pouch, and illustrates the accuracy with which predictable targets are typically centered in the catch membranes--even in the presence of other nearby targets.



FIG. 4. Separation of mealworm from adjacent 3 mm sphere by Lasiurus borealis. The bat is here using a backward somersault technique (ref. #12) for target capture. Both the sphere and another mealworm were within a few centimeters of the selected target at the time of capture. High-speed films show that even when two adjacent targets are captured, only the pre-selected target is normally seized with the mouth.



FIG. 5. Attempt to capture mealworm against surface by Myotis lucifugus. The bat accurately tracked the target to the surface but failed to complete catch while preparing for contact with the surface. (For discussion, see text.)

Complex clutter echoes

Figure 6 shows a bat (*Myotis lucifugus*) about to catch a mealworm close to clusters of yew needles which individually produce echoes not too dissimilar from those returned by a mealworm.

Figure 7 shows a successful catch by the same bat within a space between yew branches. Note that the bare twig in the center was brushed by the bat's wing as it entered the space.

Echo evaluation in the presence of competing signals

Figure 8 shows the approach of two bats from approximately opposite directions toward a single mealworm. In this situation the bat must contend with two sets of incoming signals that are stronger than the echoes of the emitted signals returning from the mealworm: first, echoes from the opposing bat, and second, the very strong signals coming directly from the opposing bat. Apparently, however, these competing signals fail to impair the bat's echolocating proficiency.

Figure 9 shows a typical result. In this instance the two bats attempted simultaneous catches of the same target--with no detectable loss of accuracy. The mealworm can be seen starting to fall out from between the two bats at the second of the two flash images.

Constraining configurations

Figure 10 shows the successful capture of a mealworm as the bat flew through spaces between hemlock twigs. Here the clutter echoes were less massive than with the denser clutter backgrounds tested. However, evaluation of the space configuration relative to the target's trajectory was required. Though the bats often brushed against the foliage or twigs (as seen here by the vibration of the fine set of twigs), severe collisions with injurious twigs, or other objects, were never seen.



FIG. 6. Myotis lucifugus about to catch mealworm close to tips of
yew needles. (For discussion, see text.)



FIG. 7. Capture of mealworm by Myotis lucifugus in space between yew branches. In order to reach the mealworm the bat brushed the bare twig in the center. Echoes were here being returned by portions of the clutter configuration that were closer to the bat than the target.



FIG. 8. Approach of two Myotis lucifugus toward one target. Each bat must here separate the faint target echo from the larger echo from the opposite bat and from the intense signals it is emitting.



FIG. 9. Simultaneous attempts to intercept one target by the two bats of Fig. 8. In spite of the interference noted in the situation of Fig. 8, both bats were able to attempt accurate seizures of a single target. Unless one bat reached the target slightly ahead of the other bat, the target typically fell out from between the two colliding bats, as seen here.



FIG. 11. Somersault catch by Lasiurus borealis at edge of pine branch. This bat commonly made catches close to configurations of foliage, but executed its interceptions so as to brush past--but never collide with--the foliage.



FIG. 10. Capture of mealworm against small hemlock twig by Myotis lucifugus. Although the magnitude of the echoes produced by the clutter configuration was much less than in Fig. 7, the bat had to execute its interception within the space constraints of the surrounding twigs. (Small twig touched during target seizure can be seen vibrating.)

Figure 11 shows the successful (somersault) catch of a mealworm by a red bat as it approaches a space between tufts of white pine needles.

Figure 12 illustrates another solution to the problem of pursuit when the target is too close to an interfering configuration. Here the bat tracked a moth as it flew along the edge of a pine branch and captured it shortly after it flew out (not shown in picture).

SOME RELATED PERFORMANCE CONSIDERATIONS

The illustrations presented were derived in part from photographed portions of systematic tests and in part from sample photographs of a variety of pursuit situations in the presence of interference. Not illustrated were the systematic results which indicated that the proclivity for pursuit and the accuracy of its completion were related to the facility or adequacy of initial detection and trajectory evaluation. Once good "lock-on" and effective target following were established, clutter sources appeared to produce little decrease in interception proficiency--though the possibility of potential collision often appeared to produce relinquishment of pursuit. Detection, however, was sometimes dependent upon adequate initial separation of a moving target from a large clutter-producing background. With fast-moving bats at least, the interference-suppressing mechanisms did not appear to become effectively operative unless adequate initial separation of target echoes and clutter echoes was achieved.

The observed pursuit performances of bats under conditions involving various kinds of interference also appear to depend, in part, upon important features of the bats' normal techniques. Among the more



FIG. 12. Preparation for delayed catch of moth by Myotis lucifugus.

The bat here made no attempt to seize the moth as it flew in close proximity to the pine branch. Capture was accomplished, however, shortly after the moth flew out from the branch (not shown in picture). Note that bat continues to track the target accurately as it passes close to the branch.



FIG. 13. Erroneous seizure of pine needle by Myotis lucifugus.

The needle was flicked upward by the bat's tail membrane and can be seen curving into the central space as the bat goes into its catch maneuver (upper image). Prior to this attempt, a number of fruit flies had been flying in the vicinity of the needles. Inset shows the comparative sizes of needles and fly. Such erroneous catches appeared to be limited to one or two bats.

significant features of the bats' methods, the following should be mentioned: localization accuracy, predictive capability, response speed, quickness and precision of motor control, and adaptive capacities.

Localization accuracies and predictive capacities

While it is possible to make direct observations from photographs of the approximate accuracy of the aim of a bat's head, evaluation of a bat's range accuracy is more difficult. A rough approximation to the accuracy of head aim (in azimuth and elevation) for Myotis lucifugus was made with the use of two photographic observers. One observer selected a number of photographs made almost directly from the side or from almost directly above or below and presented them to the other observer with the target covered. The second observer was then asked to draw a line in the estimated direction of the bat's target localization. When actual and estimated target directions were compared, the results suggested that the bat's accuracy of head aim mostly fell within $\pm 5^\circ$ of the actual target position.

Head aim, however, is not an infallible indicator of localization accuracy. At close range, bats often cease to follow the targets with their heads. Red bats, for example, often maintain a constant orientation of the head while apparently making accurate evaluation of the relative position of a maneuvering moth (12). It is thus clear that the capacity of bats to localize discrete objects is at least as good--and often much better--than the observed accuracy of head aim.

In the presence of nearby clutter echoes, a bat's attention was sometimes diverted to some nearby feature that produced an echo of typical target size (Fig. 13), but as long as target following was

maintained, loss of localization accuracy for a selected object seldom seemed to be impaired.

To estimate a bat's accuracy of range determination, while at some distance from the target, two methods have sometimes been employed. The first is by signal shift, and the second by analysis of predictive accuracy. The pursuit signals of bats, during approach to a predictably moving target, tend to fall into several phases or stages--sometimes defined as evaluation, approach and terminal phases (11). Shortly after target detection the bats' signals were sometimes characterized by a repetition rate plateau (evaluation or initial approach phase), after which a sudden acceleration of pulse rate (final approach phase) took place. In certain bats the initiation of this pulse-acceleration phase occurred about 200 milliseconds prior to target capture, with a range of deviation that fell mostly within ± 10 to 20 milliseconds of the central value. Since the bat's approach speed was relatively constant (at about 5 meters per second)--and since the target position varied considerably from any fixed reference point--the bat apparently initiated the pulse acceleration phase with an accuracy of 10 to 20% of the actual distance to capture. Instantaneous range localization must have been as good as this or better--particularly since predictive estimates of catch-point were normally required.

Estimation of range accuracies by use of the bats' predictive evaluations is based on observations of the bats' capacity to judge in advance an effective pursuit path for capture of an accelerating or maneuvering target. Figure 14 (adapted from Fig. 2 of ref.12) shows the capture of a downward spiralling moth by a red bat. The significant

feature of this pursuit was the bat's evaluation of the position of the moth relative to the irregular surface (grass and low shrubs) about one meter below the predicted capture point. Had the bat been unable to make a relatively accurate evaluation of the range to the moth--from approximately two meters away--a successful pursuit would have been difficult to initiate. In less than half a second, the bat rolled onto its back, dove down to roughly the moth's level, rolled out again and made its capture along a path parallel to the ground. As previously noted, such photographs of pursuit in the presence of constraining configurations seldom indicate any loss of target localization accuracy, as compared with accuracies seen in the absence of interference. This does not imply, however, a corresponding accuracy of localization for the various features of the constraining backgrounds. Perhaps the best guess would be that such localizations are only as accurate as required for the establishment of a suitable flight path. No attempt has been made, however, to quantify the accuracy of such localizations.

Speed and accuracy of response

Response speeds and reaction times to acoustical stimuli have not been systematically measured. Moreover, since the flash interval of most pursuit photographs was 1/10 second, the time-intervals of events occurring at less than this spacing were determinable only from sample high-speed films. Existing evidence suggests that accurate head aim is commonly established within less than 1/10 second after initial detection. Response to an unexpected shift of a target appears to occur in about 1/20 second, but may be less.



FIG. 14. (adapted from Fig. 2 of ref. #12). Capture of moth near the ground by Lasiurus borealis. The moth was here spiralling toward the grass (about a meter below), thus requiring the bat to dive and then level off in order to accomplish the interception at speed without danger of collision. (The bat's velocity was about 6 meters per second.)

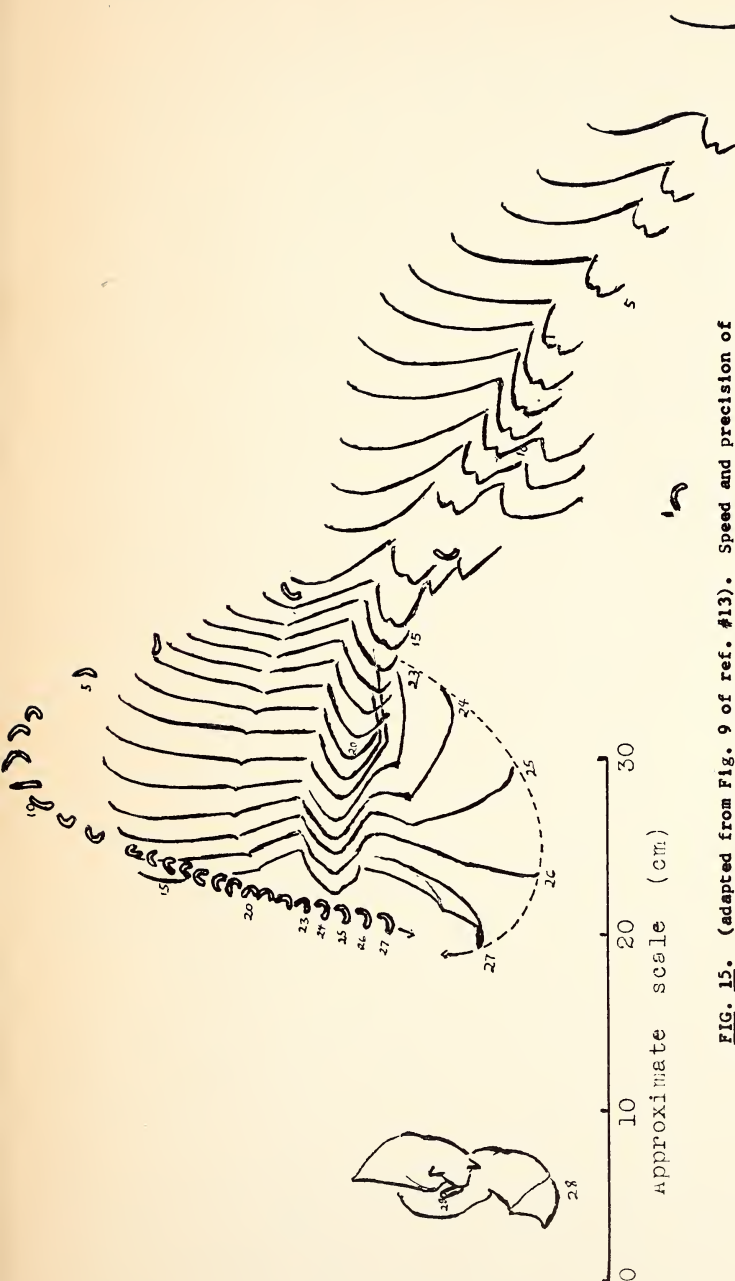


FIG. 15. (adapted from Fig. 9 of ref. #13). Speed and precision of wing action during target seizure. This sequence was traced from a set of images made by the bat's own emitted pulses, and thus, in a sense, represents the bat's own view of its interception. A significant feature here is the rate of travel of the bat's wingtip (exceeding 1 cm/msec) and the accuracy with which it is placed at the required point of seizure. (Arrows from wingtip and mealworm approximate the acoustical delay to the microphone just prior to capture: i.e., the flashes were late by roughly the amount shown.)

Figure 15 (adapted from Fig. 9 of ref. 13) illustrates an example of the speed and precision of a bat's response. The set of tracings was made from a multiple flash sequence in which each flash was triggered by the pulses emitted by the bat itself. By analyzing accompanying tape recordings (in which each flash produced an artifact) measurement of flash intervals, during such sequences, was possible. However, it was necessary to take account of the acoustical delay to the pick-up microphone. In terms of the action depicted, the final acoustical delay is approximated by the length of the arrows which show the approach of wingtip and target. Perhaps the two most significant features of this illustration are: 1) the rapidity with which the final wingtip action is achieved--a 20 cm sweep of the wingtip in roughly 20 milliseconds (reaching a velocity in excess of 1 cm/msec) and 2) the final precision of placement (apparently to within roughly 1 cm³ of the required location). Since this final action is too fast for instant-to-instant control, it must have been pre-programmed on the basis of acoustical indications received and analyzed prior to its initiation.

Perhaps one of the major assets of the speed of analysis and of control response achieved by bats, relative to many biological systems, is its role in permitting the bat to deal effectively with complex spatial situations and clutter-producing configurations. Possibly the bat can relegate different aspects of its pursuit problem to different processing mechanisms, and thus attend in rapid sequence to a variety of aspects of the surrounding situation. Although behavioral and neuro-physiological approaches to such considerations have begun to provide a common informational meeting ground, much work remains before the details of the bat's methods can be formulated in any comprehensive way.

DISCUSSION

As seen in the illustrations presented, target interceptions by echolocating bats, under conditions of interference, provide interesting examples of effective action by a natural guidance system in situations of some complexity. Here the bat's system appears capable of making rapid evaluations of shifting spatial relations and also of tracking small targets when nearby objects produce competing "clutter" echoes of considerable magnitude. In the present illustrations, for example, the mean value of the clutter echoes from objects at approximately target distance sometimes reached levels 10 or 20 dB above the level of the target echoes; yet, in most instances, the bat's system suffered no detectable loss of tracking accuracy. In addition, bats demonstrated the capacity to resolve a desired target from other objects within two or three centimeters, and could do so even when echoes were being returned by many other objects in the immediate vicinity. Finally, competing signals of high intensity from other bats produced no evidence of deterioration in tracking performance. From these examples, it is clear that the bat's system demonstrates good adaptations for handling problems presented by various kinds of interfering echoes and constraining physical objects.

At the outset, certain questions were considered regarding the comparative efficacy of the guidance systems of bats and certain man-made counterparts, notably radar and sonar. Relative to synthetic echolocating systems, is the bat's system impressive--or do the man-made counterparts possess superior attributes? Taking a bionic viewpoint, two specific questions were raised: How do the performance levels compare? and 2) How do the mechanisms, and their principles of

design, compare? To make performance comparisons, it is obviously necessary to define and carry out comparable measures. However, many of the measures used in the performance analysis of synthetic systems do not legitimately apply to the bat's system--or at least not to the bat's manner of utilization of the derived indications. Measurements of detection efficiency and detection capability demonstrate good sensitivity, and experiments on the obstacle detection performance of bats under conditions of masking by wideband noise show that the bat's echo processing system is remarkably effective (7). But such measures sample only a small portion of the total capabilities of the bat's system. Moreover, they incorporate somewhat unnatural features. High levels of wideband noise seldom occur in nature, yet the results with noise masking indicate that bats can adapt their processing system so as to detect faint echoes against high levels of noise in the same frequency bands. Such measures clearly suggest certain signal processing capabilities that are at least on a par with comparable man-made systems.

More relevant to natural situations encountered by bats, however, are problems presented by clutter and physical interference. Clutter echoes are interfering echoes returned by surfaces and objects in the vicinity of some selected object of central interest. In the bat's situation, of course, such echoes are commonly associated with constraining configurations of which the bat must also take cognizance. Moreover, because the successful pursuit of insect targets under conditions of clutter and physical interference must often have been of major importance to the survival of bats, it seemed likely that a study of such performance might reveal some of the bat's more elusive capabilities. Certain of these have been illustrated here. While a

few of the observed performance features can be quantified, many aspects are difficult to define and measure in a useful way. It is possible, however, to observe what a bat can do and, to some extent, to note how the problems are handled. Recognition of such capabilities and methods can at least provide orienting steps toward more adequate analysis; and certain inferences derived from the observed performances provide useful starting points.

One of the main inferences deriving from the illustrations is the apparent capacity of bats to structure relevant aspects of the interception situation in a meaningful way, and to do so very rapidly. For the most part, a bat can identify, classify and relate relevant objects and configurations, often within a fraction of a second. Viewed in terms of figure-ground relations, it might be said that a bat can quickly establish important points of focus--such as moving targets or threatening obstacles--and can relegate to a broader, wide-angle view the background configurations which tend to affect the bat's action in more general ways.

Another inference is that the bat's system must incorporate some excellent "gating" and "filtering" functions. This inference derives in part from observations of the bat's capacity to resolve one out of several closely spaced targets, moving along similar trajectories, and in part from observations on correct localizations of targets that pass close to stationary objects or structures. Some of these objects produce echoes similar to those of the targets and some produce massive clutter echoes including echoes that may arise from objects closer to the bat than the target itself. The acoustical patterns of these echo configurations are often highly complex and

rapidly shifting. Moreover, the observed range resolutions of about 2 centimeters in the bat's selections of targets imply either a temporal resolution of the order of 75 microseconds or a capacity to interpret interference patterns that may be shifting rapidly in structure. The fact that little difference has been noted between resolutions in range, elevation and azimuth suggests that bats have effective methods of extracting spatial invariants out of complex input configurations.

Furthermore, since the bat's system can maintain its "focus" on a small, selected object, while severe clutter echoes intermittently obscure it, the system must incorporate functions akin to "property filters" and to predictive "time gates." The property filters act to identify the invariances associated with a selected target and the time gates act to exclude (from higher processing in the same functional category) all returns occurring outside the anticipated interval of echo reception. The bat's system certainly must include some very selective and sophisticated target evaluators and moving target indicators.

Related to the above inferences are those which indicate adaptive capacities for recognizing subtle echo patterns. In target discrimination experiments (14)--not illustrated here--bats were found capable of learning to distinguish a mealworm from all sizes of spheres. When trains of echoes returning from projected mealworms were photographed, it was found that a significant percentage produced only trivial shifts of echo-magnitude within the intervals used by bats to differentiate between the spheres and mealworms. The bat's system must therefore either be very sensitive to small echo-shifts or else must be

able to evaluate shape, acoustically, from perhaps a meter away. When human listeners attempted to discriminate such echoes--even at slow-down rates up to 128--no differences were detectable. The bat's system clearly has pattern sensitivities of considerable significance.

Another inference suggested by the present observations is that bats must have evolved methods of compensating for the slow unit action of neural components. Little progress has thus far been made toward an integrated description of the bat's methods. One thing is clear, however: they must relegate to a very secondary role the kinds of long sequential processing often used in radar methods. Although at the present stage of knowledge one can only guess, it seems likely that some fairly complex processing may be achieved within a dozen sequential steps.

The final inference is the evidence of adaptability noted in the bats' responses to specific targets and to background configurations. As already indicated, bats learn to identify specific targets of interest to them. They also learn the shapes and textures of configurations with which they have a chance to become familiar. For example, like other higher animals they appear to internalize a "map" of relevant features of their surroundings. Such a "map" reduces the amount of processing required in the handling of familiar spatial constraints at any instant, since the animal can presumably release stored patterns of perception and of action on the basis of minimal detected clues. However, bats often appear to require a great deal of exploration and testing in order to establish effective patterns of response to configurations which higher visual animals can evaluate almost instantly. Perhaps the small development of the higher centers in bats is a logical concomitant

of this limitation. While such slow learning may be indicative of a low intelligence level, an emphasis on certain perceptual skills and sensory-motor interrelations may have been more vital to a bat's survival. Certainly some of the auditory perceptual skills of bats appear to have reached high levels of proficiency.

The methods of natural adaptive systems have commonly been a source of scorn on the part of engineers. As indicated earlier in the present discussion, both the long-range adaptive methods of evolutionary process and the short-range adaptive procedures that operate within the life-span of individuals are judged as inefficient, wasteful and unsuitable for engineering design. The fact remains, however, that such methods have achieved certain results that engineering methods cannot match (10). It is therefore in order to review certain criticisms of natural methods and to consider whether--in spite of such criticisms--the methods may not incorporate features from which engineering designs could sometimes profit.

One obvious limitation of natural systems is "evolutionary commitment." When a biological system evolves, the design plan is maintained genetically in relatively stable form. New operating requirements cannot be met by re-design, but only by slow modifications or by incorporation of existing methods into superordinate configurations. This latter procedure tends to produce layers of mechanisms with inherent complexities--and often inappropriate design features--which the logical methods of engineering design can readily by-pass.

What bothers engineers the most, however, is the enormous inefficiency of natural methods. Only by lengthy and devious sequences of operation can design order arise. It must be gradually generated out

of countless wasteful interactions between systems of higher and lower levels of organization. For example, it has long been contended that the genetic "orders" responsible for the initial structure of human cortical tissue could account for only a small fraction of the functional connections that obviously exist in the normal adult. The ordering of these connections must therefore come about by interactions between the limited initial features of organization, important stabilities of surrounding influences and the actions generated by various functional components of the system.

Many kinds of models have been set up by investigators concerned with neural organization and adaptive pattern recognition. Efforts to design counterparts of the complex recognition systems of higher animals, however, have tended to run up against inherent limits of comprehension by human experimenters. It proves impossible, in other words, to establish meaningful mind-model couplings with systems that incorporate great complexity and diversity of operating procedures. Neurophysiologists often point out that the detailed interactions between only two or three diffuse nerve cells present analytical problems that are virtually unapproachable by conventional methods. The operation of complex interrelated clusters can scarcely be comprehended at all.

The developments of recent decades have caused biological engineers to consider what can be learned from evolutionary models. According to such methods, an experimenter no longer tries to comprehend the precise details of all the operations being carried out by the system under study. Instead, he focuses on the nature of the design rules and control influences. By the early 1950's, simplified versions of certain evolutionary models were being partially implemented with

the use of high-speed information processing devices. These models demonstrated that much could be learned about what has to be put into the design and control methods of synthetic pattern recognizing mechanisms which are based on an evolutionary type of plan. What this approach does, in effect, is to establish a set of synthetic experimenters which mediate between the human experimenter and the systems with which he works. Eventually, it may permit him to back off many steps from details of design and from specific modes of operation. Besides broadening the man-system boundary and introducing new kinds of control and observation couplings, such a "recession of the experimenter" also frees the design and test details from the time constraints of human evaluation and response.

Although it is easy to make general statements about how simple rules of operation may govern the generation of complex systems, the actual implementation of such procedures is far less simple. The general ideas must first be formulated as concepts specific enough to produce workable designs. Such designs must then be converted to forms that are compatible with existing technology. Moreover, in practice, the methods can only be designed in detail by actual tests of operation; and hence no adequate model can be formulated in detail without being actually implemented--at least in some provisional form. For illustrative purposes of the moment, we can only touch very briefly on two aspects: first, the general mode of operation of a given "functional unit" and second, a portion of the method by which specific designs of value become transferred into permanent "genetic" storage.

One way of viewing the operation of a functional unit is in terms of provisional "noise freezing." If such a unit is conceived as

an adaptive control device, its task is to identify significant features of patterns with which it is presented and to couple such identification to a required output category. The input patterns might be a selection of Morse code letters and the output choices might be divided into two possible selections or groupings, each one of which produces a selective effect upon the unit's immediate environment. (For illustrative purposes, we might imagine one output as applying left-turning increments to the autopilot of an aircraft and the other, as applying right-turning increments.)

Under initial conditions, the unit contains a number of elements, randomly connected, between which flow unordered messages. Any tendency for meaningless "order" to form spontaneously is prevented by random extraneous fluctuations which act to disrupt stable patterns of message flow. Order becomes established in the unit by the use of monitor or modifier inputs of low information content. Such inputs are akin to the reward and punishment effects of the psychologist. They act in a consistent way only when some stable aspect of the unit's environment judges momentary segments of the unit's output to be tending in a direction that is suitable for the input pattern being concurrently received. A "reward" effect acts to favor the operating configuration existing just prior to the monitor judgment. A "punishment" effect acts to suppress or shift the immediately preceding operating configuration. A rewarding effect thus acts to stabilize an operating configuration tending to connect a given recognition with a given output choice. The action comes about by methods which, in effect, "freeze" a segment of a random operating configuration which happens to carry out the required recognition and coupling. It is

important to note that the monitor or modifier system takes no cognizance of how the recognition is achieved. In this way a pattern recognition involving considerable information content may be generated by a control indication of very low information content--the "information gain" being made at the cost of a large number of useless operations.

The second concern of the moment is how the design of a unit that proves useful gets back into permanent design storage. A complete answer is beyond the present scope of discussion. However, one aspect can be pointed out. The design system generates a large number of units, all on one general plan, but varying from each other in such details as: size, connectivity, output distribution, etc. The various units are tested with a given task and only the designs of those that perform adequately are retained. By like principles of operation, the selected designs can be subjected to a smaller range of variations and perhaps the use of more specific design details. Eventually, the genetic storage contains the design of a device which is relatively well adapted for a given category of recognition. Moreover, by the use of like methods, specialized units can become linked together in "genetic" storage to generate more complex pattern recognizing functions.

Evolutionary models have a long way to go before they can either be said to represent the methods of living systems, on the one hand, or the kind of mechanism that can be effectively useful to engineers, on the other. Their importance at this stage may lie chiefly in their capacity to provide new entering wedges of comprehension and control. They also introduce new kinds of questions about living systems and may lead to better comprehension of the kinds of fundamental

differences that characterize the sensory and perceptual systems of different animals.

One important long-range question inevitably arises in any consideration of the trend of such models. When evolutionary principles act to generate successively higher levels of order out of lower levels of order, do they also tend to generate catalytic methods for the more effective ordering of order? In other words, do methods tend to arise which act to increase the efficiency as well as the effectiveness of higher levels of organization? Perhaps this is the kind of trend which leads to the effectiveness of the more versatile perceptual processes in higher animals. Although such views must obviously remain as speculations for the time being, they raise interesting questions about perceptual comparisons between the auditory recognitions of men and bats. They may also serve to indicate to conservative engineers that the very inefficiencies of animal systems may be the key to higher levels of functional effectiveness--and perhaps, in the end, even to certain kinds of functional efficiency which are not yet defined.

SUMMARY

The present discussion has reviewed the interception capabilities of echolocating bats in the presence of various kinds of interference. The illustrations suggested that the bat's guidance system could provide rapid--and often predictive--evaluations of fairly complex spatial configurations; and could do so even when the returning echoes of primary interest were greatly obscured by surrounding clutter.

An attempt was made to resolve certain of the engineering-biology controversies regarding the comparative assets of mechanized and natural "perceptual" systems. To some extent, differences arose

from differences in interest or objective. However, the higher perceptual methods and proficiencies of natural systems are hard to define in useful engineering terms. One approach to the designs of higher level perceptual systems is by way of "evolutionary models." The concepts behind such models may give significant insights as to basic perceptual differences between different animals and may eventually provide foundations for effective synthetic perceptual designs.

ABSTRACT

Examples are presented of target pursuit by echolocating bats in the presence of physical interference from nearby configurations and of acoustical interference produced by clutter echoes or the signals of other bats. Such pursuits illustrate capacities for the rapid structuring and evaluation of fairly complex spatial relations. They also suggest capacities to extract target-identifying and spatial invariances from subtle and rapidly varying echo patterns.

Some difficulties encountered in the formulation of useful models of the echo processing mechanisms of bats are reviewed, with particular reference to discrepancies of biological and engineering emphasis. Possible use of concepts associated with evolutionary models is considered. These concepts may provide new approaches to comparisons of the perceptual systems of different animals and may eventually prove of value in engineering design.

Bionic comparison
Clutter rejection
Echolocation
Evolutionary models
Perceptual organization

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IMPRIMERIE LOUIS-JEAN

Ouvrages scientifiques

TYPO - OFFSET

GAP (Hautes-Alpes)

Dépôt légal n° 89

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